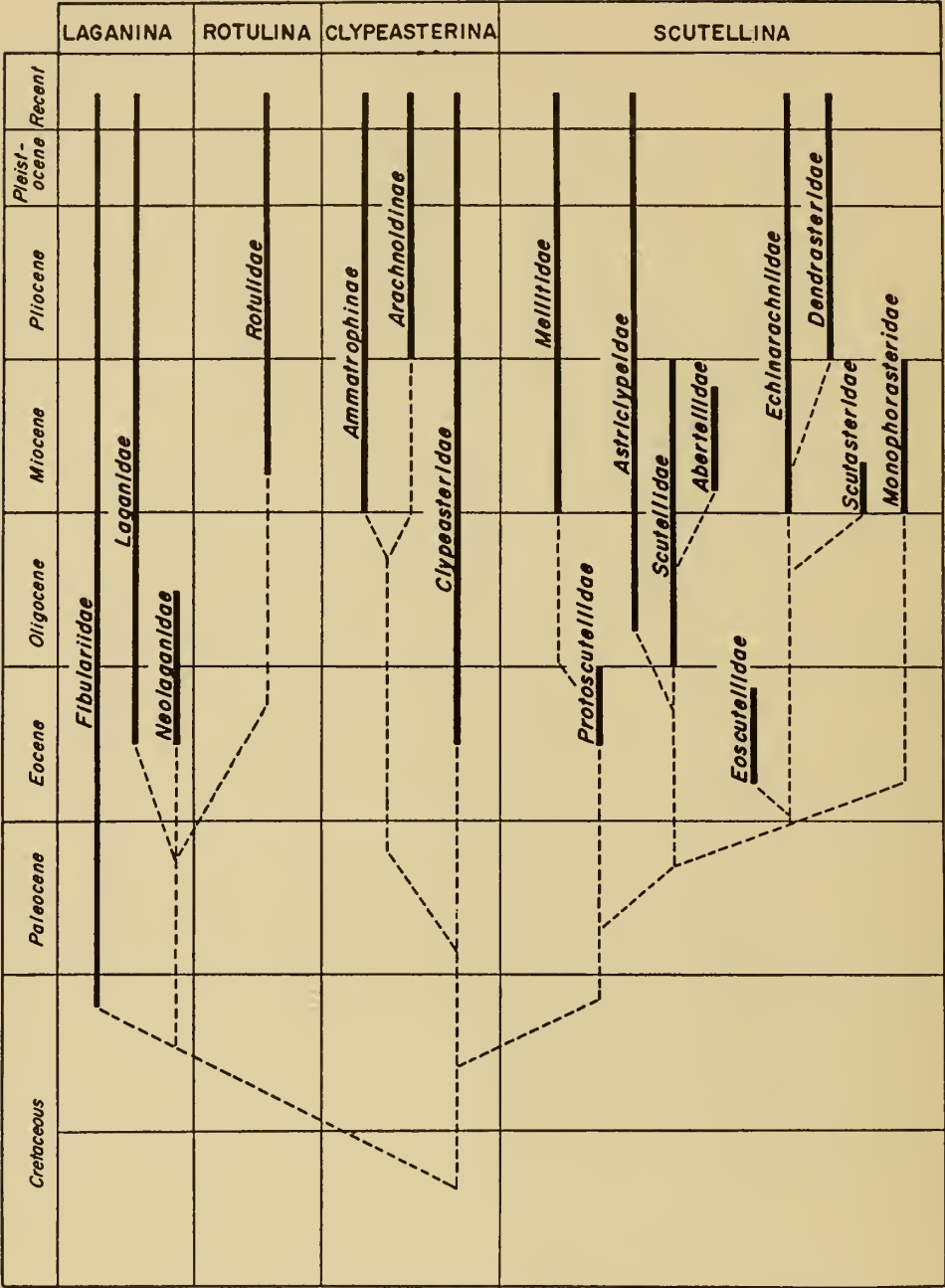




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Phylogeny of the Clypeasteroidea.



CLASSIFICATION OF CLYPEASTEROID ECHINOIDS

BY
J. WYATT DURHAM

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CLASSIFICATION OF CLYPEASTEROID ECHINOIDS

BY

J. WYATT DURHAM

(A contribution from the University of California Museum of Paleontology)

ABSTRACT

The classification and nomenclature of all supraspecific taxa within the order Clypeasteroida are reviewed and revised. Studies of individual and specific variation within the genera *Dendraster*, *Astrodapsis*, and *Echinarachnius* demonstrate that the structure of the test is extremely important in indicating relationship. Growth rings of presumable seasonal origin are widely distributed within the group and cast significant doubt on resorption as an important process in growth.

The order is divided into four suborders: the Clypeasterina, Laganina, Scutellina, and Rotulina. The Clypeasterina include the families Clypeasteridae and Arachnoididae; the latter has two subfamilies, the Arachnoidinae and Ammotrophinae. The Laganina are subdivided into the families Fibulariidae, Laganidae, and Neolaganidae. Within the Scutellina the families Scutellidae, Protoscutellidae (new), Eoscutellidae (new), Dendrasteridae, Echinarachniidae, Monophorasteridae, Mellitidae, Astriclypeidae, Abertellidae (new), and Scutasteridae (new) are recognized. The Rotulina include the single family Rotulidae.

All supraspecific taxa of the Clypeasteridae are considered synonyms of *Clypeaster* Lamarck. The following sixty-five genera referred to other families are recognized and type designations are given: *Arachnoides* Leske, *Fellaster* n. gen., *Ammotrophus* Clark, *Monostychia* Laube, *Scutellinoides* n. gen., *Fossilaster* Lambert and Thiéry, *Fibularia* Lamarck, *Fibulariella* Mortensen, *Echinocyamus* van Phelsum, *Mortonia* Gray, *Thagastea* Pomel, *Togocyamus* Oppenheim, *Cyamidia* Lambert and Thiéry, *Scutellina* Agassiz, *Porpitella* Pomel, *Eoscutum* Lambert, *Lenita* Desor, *Tarphypygus* Arnold and Clark, *Fibulaster* Lambert and Thiéry, *Laganum* Link, *Peronella* Gray, *Sismondia* Desor, *Hupea* Pomel, *Peronellites* Hayasaka and Morishita, *Rumphia* Desor, *Jacksonaster* Lambert and Thiéry, *Fibulina* Tornquist, *Neolaganum* Durham, *Cubanaster* Sanchez Roig, *Neorumphia* Durham, *Sanchezella* Durham, *Weisbordella* Durham, *Wythella* Durham, *Scutella* Lamarck, *Parascutella* Durham, *Parmulechinus* Lambert, *Protoscutella* Stefanini, *Periarchus* Conrad, *Mortonella* Pomel, *Eoscutella* Grant and Hertlein, *Dendraster* Agassiz, *Scutellaster* Cragin, *Merriamaster* Lambert, *Scaphechinus* Agassiz, *Echinarachnius* Gray, *Kewia* Nisiyama, *Vaquerosella* n. gen., *Astrodapsis* Conrad, *Pseudoastrodapsis* Durham, *Remondella* n. gen., *Tenuirachnius* n. gen., *Monophoraster* Lambert and Thiéry, *Iheringiella* Berg, *Mellita* Agassiz, *Leodia* Gray, *Mellitella* Duncan, *Encope* Agassiz, *Astriclypeus* Verrill, *Echinodiscus* Leske, *Amphiope* Agassiz, *Abertella* Durham, *Scutaster* Pack, *Rotula* Schumacher, *Heliophora* Agassiz, and *Rotuloidea* Etheridge.

Runa Agassiz, *Tournoueraster* Lambert, *Scutulium* Tournouër, *Proscutella* Pomel, and *Samlandaster* Lambert and Thiéry are not assigned to families.

In the adult rotulids ten instead of the usual five interambulacral plates are present in the basicoronal row. Presumably the extra plates are post-basicoronal plates "pushed" into the basicoronal row during ontogeny.

INTRODUCTION

THE FLATTENED "sand dollar" echinoids and their near relatives referred to the order Clypeasteroida¹ (Mortensen, 1948) are widespread as fossils in Cenozoic

¹The stem of the name *Clypeaster*, to which the appropriate terminations for families and higher categories should be added, is Clypeaster. Thus the names should be Clypeasteridae, Clypeasterina, and Clypeasteroida; not Clypeastridae, Clypeastrina, and Clypeastroida as commonly formed.

rocks and are common inhabitants of the seashore in many parts of the world. Many of them are important, short-ranged index fossils locally, and the flower-like arrangement of the petals has intrigued many a collector. Furthermore, they often occur in close-packed colonies probably numbering millions of individuals. Yet, despite their interest, significance, and abundance, the internal classification of the group has long been unsatisfactory in that the relative importance of various characters and the relationships of many genera and species are uncertain. The present paper is an attempt to clarify some of these uncertainties.

To date, most of the characters used in the classification of the clypeasteroid echinoids have been those of the externally visible morphology, the lantern, and the internal supports of the test. The character and position of the peristome; the nature and position of the periproct and, more particularly, its relationship to the ambitus; the characters of the apical system; the major features of the petals; the characters of the spines and pedicellariae; the variations in the internal supports; and the external morphology of the test—these are the principal characters that have been studied and used in the taxonomy of the group. Although Lovén (1874) long ago demonstrated the marked variation in the structural make-up of the test of different echinoids, little attempt has been made to use this variation in the classification of the clypeasteroids. Jackson (1912) used test structure to some extent in his "Phylogeny of the Echini"; but Mortensen (1948) in his volume on the Clypeasteroida makes only occasional use of this feature.

During the past five years a detailed study of the clypeasteroid echinoids has been carried forward in an attempt to improve the understanding, utilization, and classification of the group. For a few species, abundant material—in some cases hundreds of specimens from a single colony—including representatives of the type species of most supraspecific taxa (except in the family Clypeasteridae) and specimens of a majority of the named species (again excepting the family Clypeasteridae) of the order Clypeasteroida have been available for examination.

The results of these studies indicate that the test structure is of primary importance in indicating relationships among these echinoids, and that seemingly minor external characters may be indicative of highly significant structural differences.

During the past sixty years much reliance has been placed on the numerous excellent-appearing and presumably reliable illustrations in Cotteau's volumes (1889–1894) on the Eocene echinoids of France. During the present study, topotypes of many of the species he figured have been available for study. For most parts of the test his figures were accurate, but the details (when shown) of the head of the ambulacral and interambulacral areas and of the basicoronal plates around the peristome were found to be very unreliable. In the fibulariids, for instance, Cotteau invariably indicates the presence of two columns of plates at the head of the interambulacral areas, but in all species examined there is only a single plate, or a series of single plates, in this position. Similar discrepancies with respect to some other details of his illustrations have also been found.

Grateful acknowledgment is due Dr. Elisabeth Deichmann, Dr. C. Wythe Cooke, Dr. Mario Sanchez Roig, Dr. Richard V. Melville, Dr. Leslie Bairstow, Dr. André Chavan, Dr. Martin F. Glaesner, Dr. Syôzô Nisiyama, Dr. Emery F. Swan, and Mr. Maurice H. Wallace for aid in obtaining material for study. Mr. José Corvalán Díaz has aided in the studies of variation in *Echinarachnius parma* Lamarek.

THE CLYPEASTEROID TEST

EXTERNAL MORPHOLOGY

The test of the clypeasteroid echinoids varies in shape from ovoid, in genera such as *Echinoeyamus*, to a flattened disc in the typical "sand dollars" or "sand shillings" such as *Dendraster* or *Arachnoides*. Usually, even in the more flattened species, the aboral surface is more or less arched or peaked or vaulted. Except in the primitive genera, the oral surface is usually flattened. In some genera, such as *Clypeaster*, there may be an infundibulum around the mouth; in others, such as *Seutella*, the oral surface is flat to slightly concave. In some echinoids, such as *Lenita* or a local population of *Dendraster excentricus* (False Bay, San Juan Island, Washington), the oral surface is saddle-shaped in a large number of individuals; but this is rare.

The apical system is on the aboral surface and is usually approximately central in position; but in some genera, such as *Dendraster*, it may be somewhat posterior. The mouth, or peristome, is also approximately central in position but is on the lower, or oral, surface. The periproct occupies a position in the posterior interambulacrum between the apical system and the peristome but is never close to the apical system. Orally, the periproct may approach very close to the peristome, as in *Mellita*. The periproct is never large and is not situated in a depression, although in genera such as *Arachnoides*, in which it is close to the margin, there may be a notch in the margin adjacent to the periproct.

In the more flattened genera, the ambitus becomes prominent and is a highly significant reference point, both for the external morphology and for the structure of the test. Marginally, it may be more or less rounded, as in the various laganid genera, or it may be sharp, angular, and thin, as in *Eoscutella* or *Echinodiscus*.

On the aboral surface, the apical parts of the ambulacral areas containing the pores for the respiratory tube feet are formed into more or less distinct petals (fig. 1). In the small primitive fibulariid genera the petals are poorly defined and at times hardly recognizable (e.g., *Fibularia cribellum*, Mortensen, 1948, fig. 95). However, in the more advanced genera the petals are very distinct (fig. 1, *j-m*); they may be closed and sharply delimited from the rest of the area (e.g., *Dendraster*) or open and gradational (e.g., *Rotula*, fig. 1, *b*). Within the petals, the pore-pairs for the primary tube feet are paired and may have a groove connecting the pores (conjugate, fig. 1, *b-d, f-m*), or lack it (nonconjugate, fig. 1, *e*). In the nonconjugate genera, the individual pores are similar and are generally round in outline. In the conjugate group, the outer pore may be greatly elongated, and on close inspection it is often found to have several partitions subdividing it deep within the pore. Small pores for the secondary tube feet are numerous and present on both oral and aboral surfaces, sometimes concentrated along the sutural areas between the ambulacral plates or in the food grooves when these are well developed, but at other times more widespread (fig. 2, *e* and *f*), even extending into the interambulacral plates, as in the arachnoidids.

In genera such as *Echinocyamus* there are no apparent food grooves leading to the peristome, but in more advanced members of the order a more or less complex

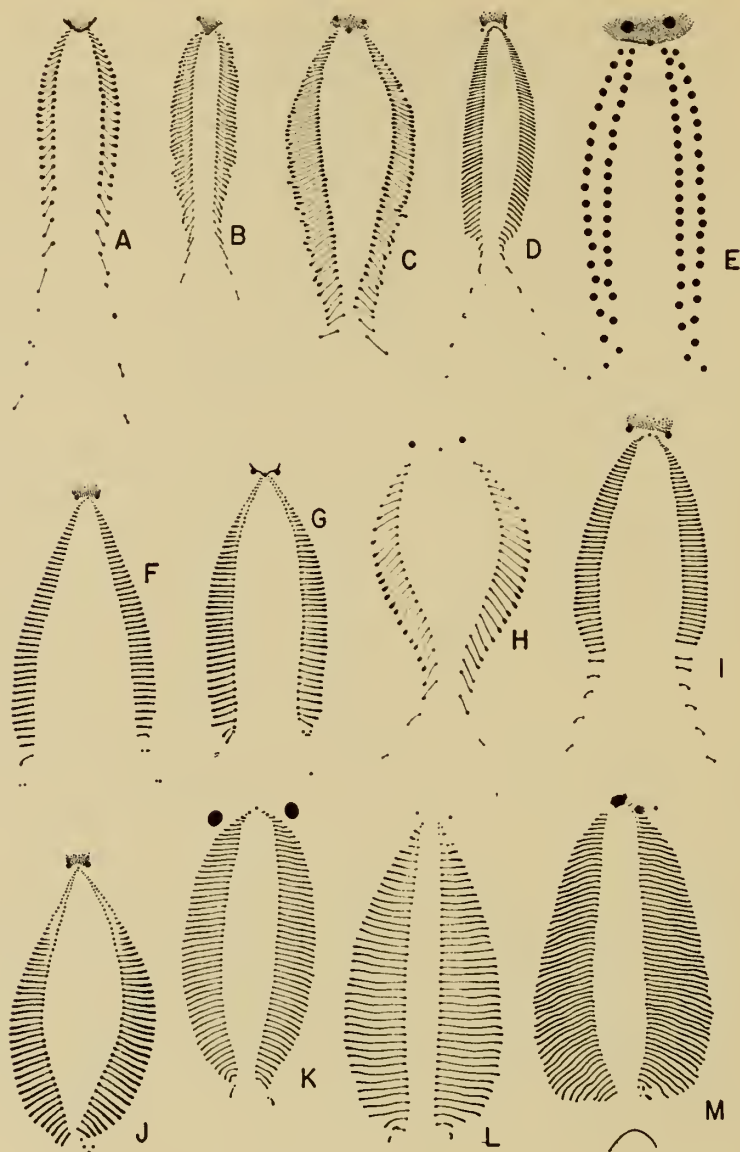


Fig. 1. Clypeasteroid petals: *a*, *Heliophora orbiculus* (Linnaeus), $\times 2.8$, anterior petal. *b*, *Rotula deciesdigitata* (Leske), $\times 1.8$, left posterior petal. *c*, *Laganum laganum* (Leske), $\times 2.4$, right anterior petal. *d*, *Dendraster excentricus* (Eschscholtz), $\times 0.88$, left anterior petal. *e*, *Mortonia australis* (Des Moulins), $\times 8.6$, left anterior petal. *f*, *Fellaster zelandiae* (Gray), $\times 2.1$, left anterior petal. *g*, *Clypeaster ravenelii* (A. Agassiz), $\times 1$, left anterior petal. *h*, *Jacksonaster depressum* (Lesson), $\times 2.3$, left anterior petal. *i*, *Echinarachnius parma* (Lamarek), $\times 2.3$, left anterior petal. *j*, *Clypeaster prostratus* (Ravenel), $\times 1.9$, left anterior petal. *k*, *Leodia sexiesperforata* (Leske), $\times 2.5$, left anterior petal. *l*, *Mortonella quinquefaria* (Say), $\times 2.5$, left anterior petal. *m*, *Astriclypeus manni* (Verrill), $\times 1.7$, right posterior petal.

system of grooves (figs. 2-4) leads to the peristome. In genera such as *Laganum* (fig. 2, *c*) they consist of a simple groove in each ambulacrum extending part way to the margin; in others, such as *Encope* (fig. 4, *b*), it is a much more complex

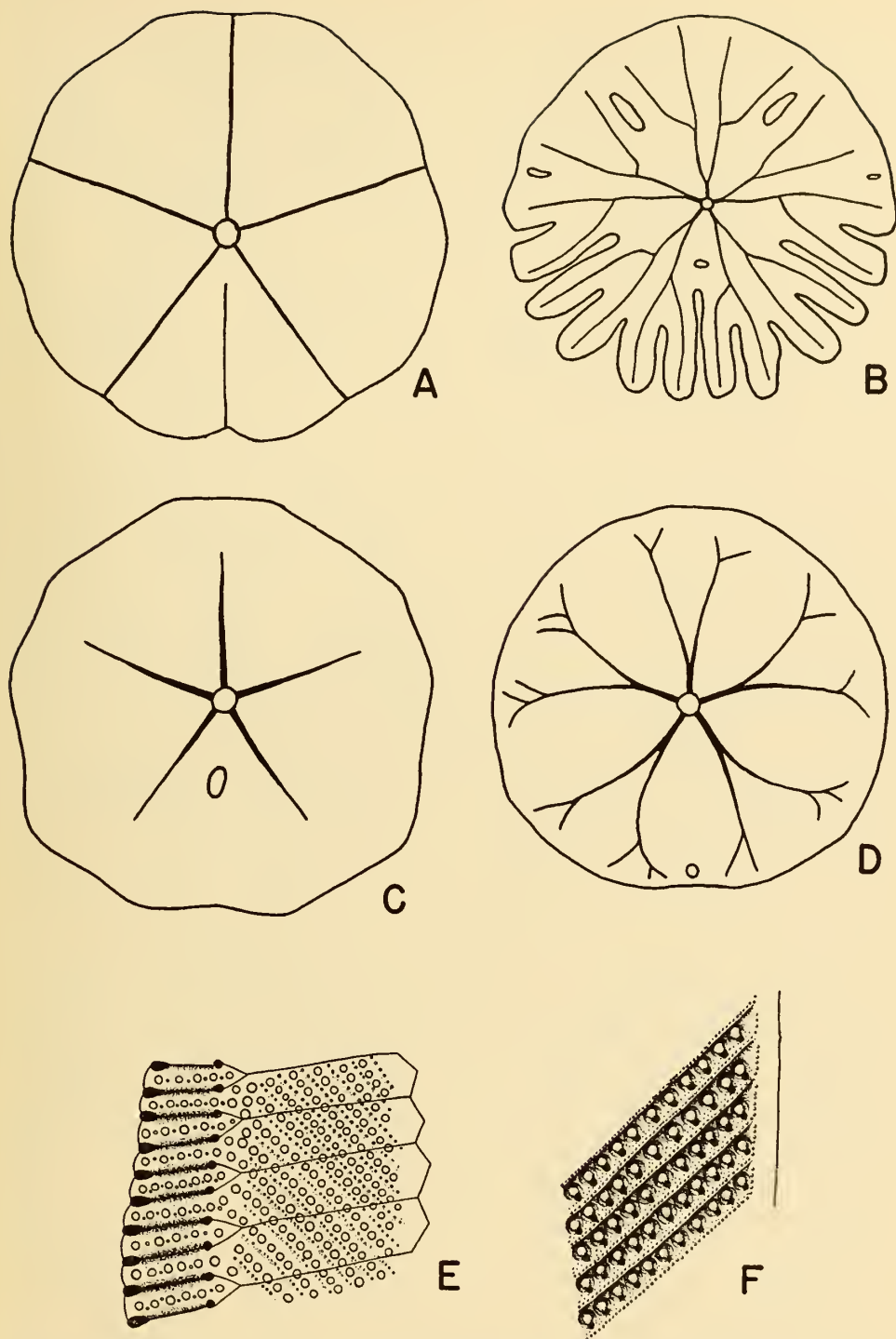


Fig. 2. Ambulacral food grooves and combed areas: *a*, *Arachnoides placenta* (Linnaeus), $\times 1.2$, after hypotype no. 33351; Recent, east coast of Sumatra. *b*, *Rotula deciesdigitata* (Leske), $\times 0.85$, after hypotype no. 33852; Recent, Loanda, Angola. *c*, *Laganum laganum* (Leske), $\times 0.9$, after hypotype no. 33258; Recent, New Hebrides. *d*, *Iheringiella patagoniensis* (Desor), $\times 0.86$, after Lahille (1898, pl. 2, fig. 9). *e*, *Arachnoides placenta* (Linnaeus), $\times 6$, combed area in petal, after Mortensen (1948, fig. 80), $\times 6$. *f*, *Arachnoides placenta* (Linnaeus), $\times 6$, ambulacral combed area on oral surface, after Mortensen (1948, fig. 79).

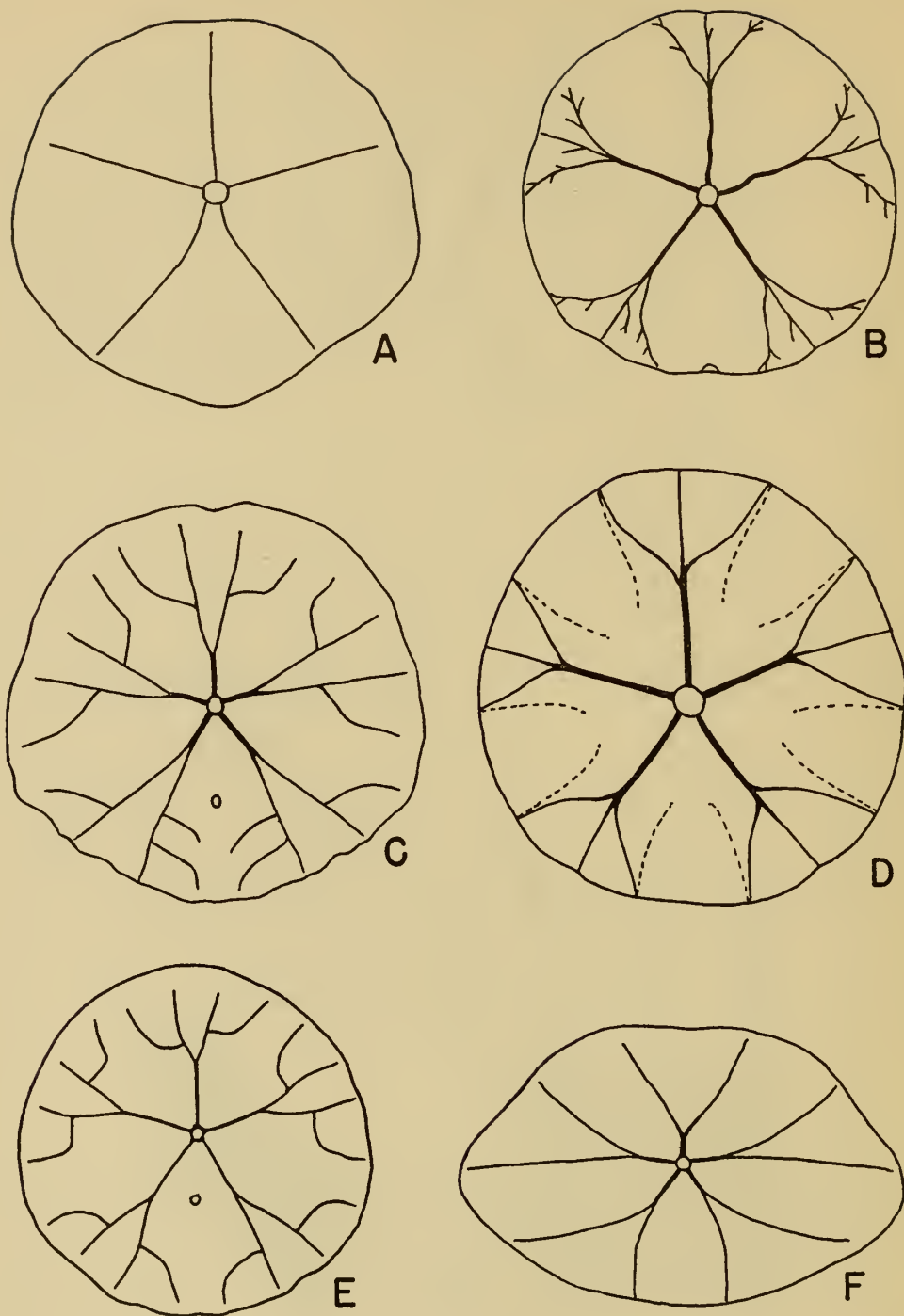


Fig. 3. Ambulastral food grooves: a, *Kewia fairbanksi* (Arnold), $\times 1.25$, after hypotype no. 13711; lower Miocene, California. b, *Echinarachnius parma* (Lamarek), $\times 0.75$, after hypotype no. 32933; Recent, Kodiak Island. c, *Scutella subrotunda* (Leske), $\times 0.57$, after British Museum (Natural History) topotype no. E 16593, from same specimen as fig. 1 of Lambert, 1912; "Oligo-Miocene," Malta (courtesy of the British Museum and Richard V. Melville). d, *Astrodapsis antiselli* Conrad, $\times 1$, after hypotype no. 11030; lower Pliocene, California. e, *Periarchus lyelli* (Conrad), $\times 0.6$, after W. B. Clark and Twitchell (1915, pl. 61, fig. 2, b); Eocene, Alabama. f, *Eoscutella coosensis* (Kew), $\times 0.8$, after hypotype no. 33388; upper Eocene, Oregon. Details of secondary food grooves (if present) not discernible.

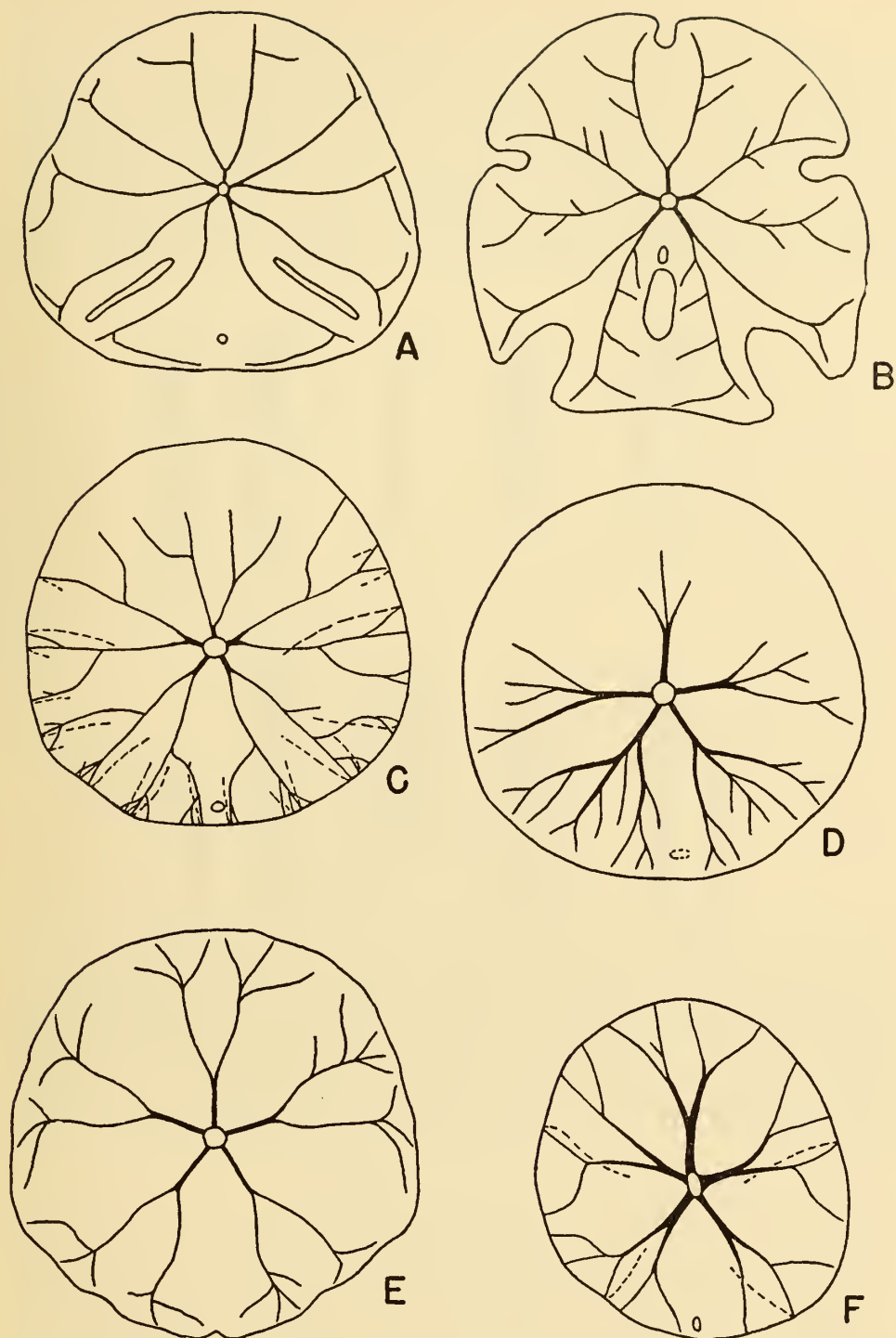


Fig. 4. Ambulaeal food grooves: a, *Echinodiscus bisperforatus* Leske, $\times 0.8$, after hypotype no. 33790; Pliocene, India. b, *Encope grandis* L. Agassiz, $\times 0.6$, after hypotype no. 33862; Recent, Gulf of California. c, *Dendraster excentricus* (Eschscholtz), $\times 0.8$, after hypotype no. 32934; Recent, Puget Sound. d, *Scutellaster oregonensis major* (Kew), $\times 0.8$, after "cotype" no. 11352; Pliocene, California. e, *Scaphechinus mirabilis* forma *japonica* (von Martens), $\times 0.9$, after hypotype no. 33359; Recent, Tokyo Bay. f, *Merriamaster perrini* (Weaver), $\times 0.95$, after hypotype no. 11062; Pliocene, California.

system of grooves extending onto the interambulacral areas as well, but with a central trunk on each ambulacrum leading to the peristome. In most genera the food-groove system is restricted to the oral surface; but in some genera, such as *Astrodapsis* (fig. 3, *d*) and *Dendraster* (fig. 4, *c*), it extends onto the aboral surface as well. The food grooves are, for the most part, symmetrical about the peristome, but in those genera which in life often assume a semivertical position on the sea floor—*Dendraster*, for instance—the food-groove system may be much more extensively developed posteriorly than anteriorly.

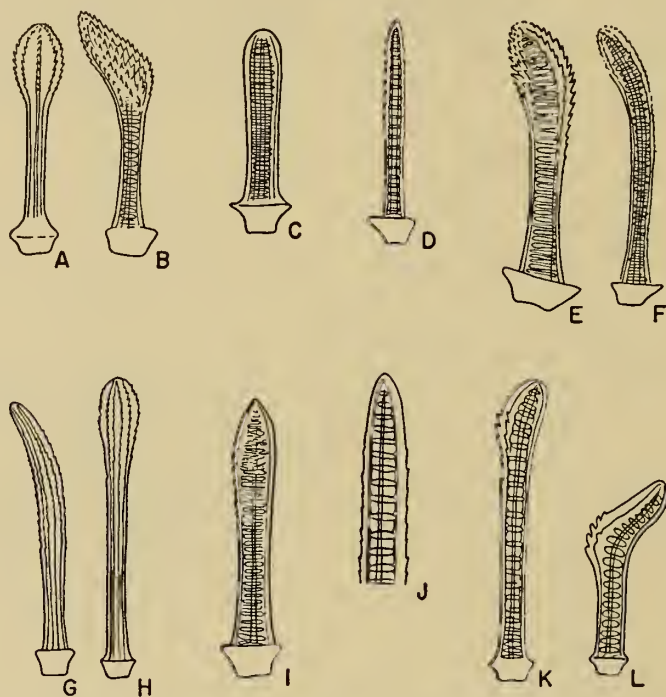


Fig. 5. Primary spines of clypeasteroid echinoids: *a*, *Scaphechinus mirabilis* A. Agassiz, $\times 45$, aboral. *b*, *Dendraster excentricus* (Eschscholtz), $\times 55$, aboral. *c*, *Mortonia australis* (Des Moulins), $\times 25$. *d*, *Fibularia ovulum* Lamarek, $\times 45$. *e*, *Echinodiscus bisperforatus* Leske, $\times 80$, aboral. *f*, *Echinodiscus bisperforatus* Leske, $\times 80$, oral. *g*, *Arachnoides placenta* (Linnaeus), $\times 40$, interambulacral. *h*, *Arachnoides placenta* (Linnaeus), $\times 55$, from combed area. *i*, *Clypeaster rotundus* (A. Agassiz), $\times 55$, aboral. *j*, *Jacksonaster depressum* (Lesson), $\times 100$, point only. *k*, *Heliophora orbiculus* (Linnaeus), $\times 75$, aboral. *l*, *Rotula deciesdigitata* (Leske), $\times 75$, aboral. After Mortensen, 1948, figs. 218, *a*; 218, *b*; 102, *a*; 102, *c*; 219, *a*; 219, *b*; 86, *c*; 13, *c*; 161, *b*; 255, *a*.

In life, the test is covered by a more or less dense coat of small, short spines of two types, the primary and the miliary. The primary spines (fig. 5) are heavier and somewhat longer than the miliary spines and usually are not more than 5 mm. long. The cross section of the primary spines (fig. 26) is significantly different in the various groups. The primary spines vary from fusiform to club-shaped, often with considerable variation in different species of the same genus. At times, the terminal "club" is so expanded as to form a "pavement" (A. H. Clark, 1946, pls. 1 and 2 upper). The miliary spines are much more numerous, slenderer, and

shorter than the primary spines. Three principal types (fig. 6) of miliary spines occur and are characteristic of different suborders. In one, the clypeasterinid type, the spine is simply serrate and pointed distally (fig. 6, *a-c*); the second, or laganinid, type has a well-developed crown (fig. 6, *f-h*) terminally; in the third, or scutellinid, type (fig. 6, *d, e, j*), the spine is serrate distally and in life terminates in a glandular sack. The character and type of spines, both primary and miliary, may vary over different areas of the test, particularly from the oral to the aboral side, and from ambulacral to interambulacral areas on the oral surface.

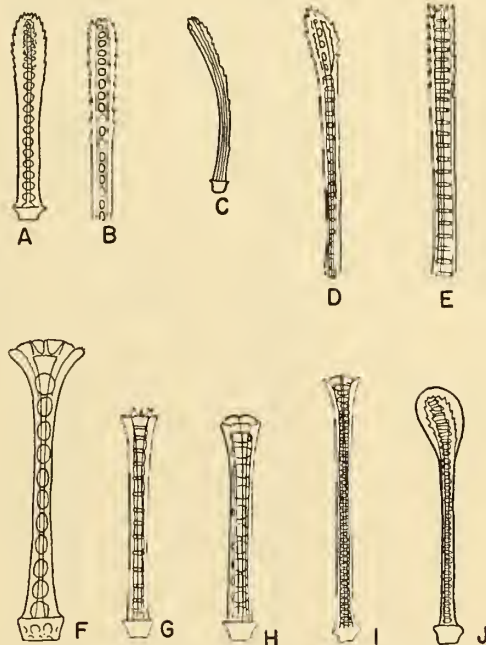


Fig. 6. Miliary spines of clypeasteroid echinoids: *a*, *Clypeaster japonicus* Döderlein, $\times 55$. *b*, *Clypeaster rotundus* (A. Agassiz), $\times 65$. *c*, *Arachnoides placenta* (Linnaeus), $\times 55$. *d*, *Scaphechinus mirabilis* A. Agassiz, $\times 100$, aboral. *e*, *Echinarachnius parma* (Lamarek), $\times 100$, aboral. *f*, *Peronella japonica* Mortensen, $\times 150$. *g*, *Fibularia ovulum* Lamarek, $\times 105$. *h*, *Mortonia australis* (Des Moulins), $\times 105$. *i*, *Heliophora orbiculus* (Linnaeus), $\times 75$. *j*, a scutellinid, $\times 75$. After Mortensen, 1948, figs. 14, *b*; 14, *c*; 86, *a*; 208, *d*; 208, *a*; 180, *b*; 102, *d*; 102, *b*; 225, *b*; 2, *c*.

The tubercles for the attachment of the primary spines are perforate in most members of the order, but it is difficult to determine whether or not the tubercles of some of the characteristically small species of some genera are perforate. Some, at least, have the tubercles distinctly crenulate. The density of the tubercles may vary greatly in different species of the same genus. According to Mortensen (1948, pp. 1-2), tridentate, ophicephalous, triphyllous, and globiferous pedicellariae (fig. 7) occur in the order, but the last-named type has been recorded only in the genus *Fibulariella*.

No gill slits are present on the peristome, and there are no external gills. Phylloides and bourrelets are likewise absent. The sphaeridia are single or double and are close to the peristome in the ambulacral mid-line. The buccal membrane may be either naked or covered with irregular calcareous plates (fig. 8, *d, h*). Calcareous

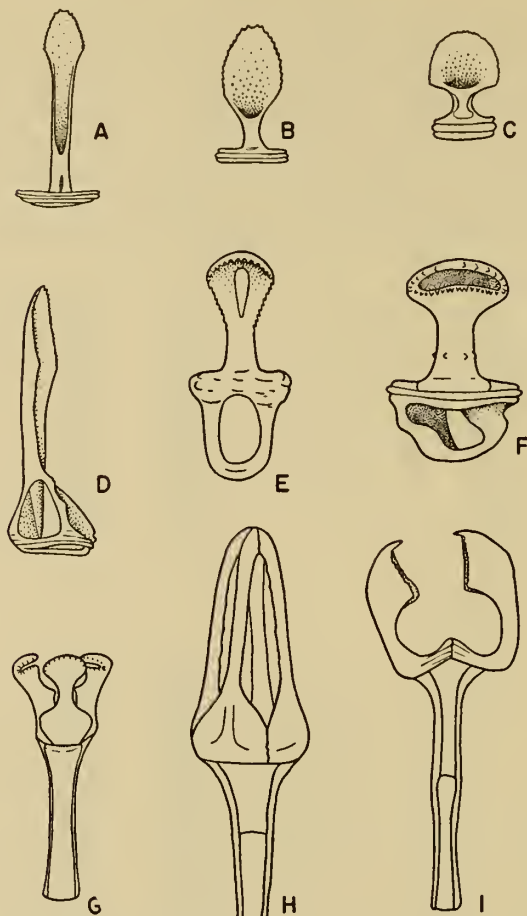


Fig. 7. Pedicellariae of clypeasteroid echinoids: *a*, *Jacksonaster depressum* (Lesson), $\times 80$. *b*, *Laganum fudsiyama* Döderlein, $\times 125$. *c*, *Clypeaster australasiae* (Gray), $\times 180$. *d*, *Clypeaster fervens* Koehler, $\times 42$. *e*, *Laganum dickersoni keiense* Mortensen, $\times 125$. *f*, *Clypeaster australasiae* (Gray), $\times 180$. *g*, *Clypeaster rarispinus* de Meijere, $\times 70$. *h*, *Clypeaster subdepressus* Gray, $\times 27$. *i*, *Leodia sexesperforata* (Leske), $\times 160$. Figs. *a*, *d*, and *h*, tridentate. Figs. *b* and *c*, triphyllous. Figs. *e*, *f*, and *g*, ophiocephalous. Fig. *i*, "bidentate." Figs. *a-f*, single valves; *g-i*, complete valves. Fig. *h*, a four-valved, tridentate type. Modified after Mortensen, 1948, pl. 70, figs. 20, 15; pl. 65, figs. 6 and 7; pl. 70, fig. 13; pl. 65, fig. 3; pl. 64, fig. 8; pl. 65, fig. 14; pl. 72, fig. 19.

spicules (fig. 8, *a-c*, *e-g*) may be imbedded in the buccal membrane or present terminally in the locomotory tube feet. The periproct may be naked or covered by a varying number of small calcareous plates (fig. 8, *i-k*).

INTERNAL MORPHOLOGY

In all except some of the presumably primitive fibulariids, internal calcareous supports for the test are more or less well developed. In general, the complexity of these supporting structures appears to be a function of the degree of flattening the test has undergone. In the simpler cases, as in *Echinocyamus*, the supports consist of five pairs of more or less extensive partitions (see Mortensen, 1948, fig.

96, c) extending from the ambitus inward toward the auricles in an interambulacral position. In the more complex cases, as in *Clypeaster rosaceus* (Mortensen, 1948, fig. 17) or *Dendraster excentricus* (Durham, 1949, pl. 2, fig. 4), the pillars and partitions are exceedingly complex in their distributional pattern and abundance. The complexity may vary considerably in different species of the same genus, as in *Dendraster gibbsii* and *D. excentricus* (Durham, 1949, pl. 2, pp. 2, 4), or in different genera of the same family, as in *Dendraster* and *Merriamaster*

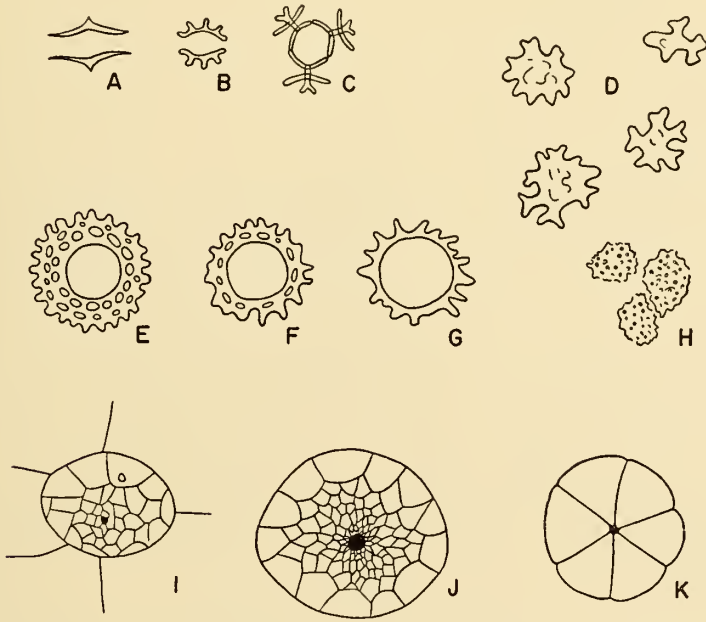


Fig. 8. Spicules, buccal plates, and periproctal plates of clypeasteroid echinoids: a, *Echinarachnius parma* (Lamarek), $\times 180$, spicules from sucking disc of tube foot. b, *Echinodiscus auritus* Leske, $\times 210$, spicules from sucking disc of tube foot. c, *Heliophora orbiculus* (Linnaeus), $\times 265$, spicules from sucking disc of tube foot. d, *Clypeaster rotundus* (A. Agassiz), $\times 100$, spicules from buccal membrane. e, *Clypeaster rangianus* Des Moulins, $\times 135$, spicule from sucking disc of tube foot. f, *Clypeaster rotundus* (A. Agassiz), $\times 180$, spicule from sucking disc of tube foot. g, *Clypeaster latissimus* (Lamarek), $\times 180$, spicule from sucking disc of tube foot. h, *Heliophora orbiculus* (Linnaeus), $\times 70$, plates from buccal membrane. i, *Fellaster zelandiae* (Gray), $\times 10$, periproctal plates. j, *Peronella japonica* Mortensen, $\times 10$, periproctal plates. k, *Echinocyamus longatus* H. L. Clark, $\times 15$, periproctal plates. After Mortensen, 1948, figs. 211, a; 211, d; 211, e; 12; 16, b; 16, c; 16, e; 206; 84, c; 178, c; 101, c.

(Durham, 1949, pl. 2). According to Mortensen (1948, p. 162), internal supports are completely absent in the genus *Fibularia*. In *Mortonia australis* only the posterior pair of partitions, enclosing the periproct, are present, and even these are only slightly developed.

Arising from the interior of the test are the auricles (fig. 9), the processes to which the muscles supporting the lantern are attached. In the clypeasterids and arachnoidids the ten auricles are separate (fig. 9, c, e, f) and attached to the marginal edges of the basicoronal ambulacral plates. Since the basicoronal interambulacral plates are very small in these families, they may not reach the interior surface of the test, and the auricles are very close together. In the other families

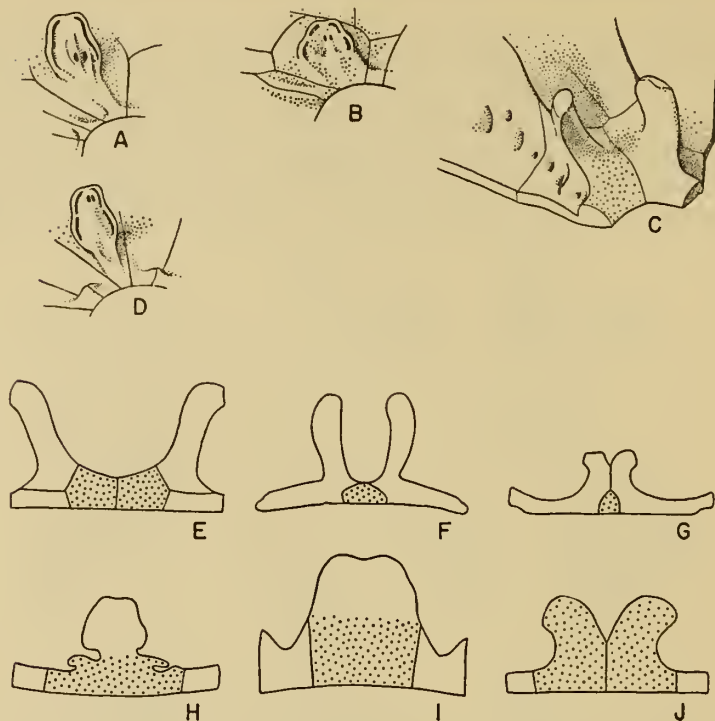


Fig. 9. Auricles and apophyses of various echinoids: *a*, *Echinarachnius parma* (Lamarek). *b*, *Echinocyamus pusillus* (Müller). *c*, *Clypeaster ravenelii* (A. Agassiz), hypotype no. 33860. *d*, *Hupea decagonalis* (Lesson). *e*, *Tripeustes* (profile). *f*, *Clypeaster* (profile). *g*, *Arachnoides* (profile). *h*, *Encope* (profile). *i*, *Echinocyamus* (profile). *j*, *Cidar* (profile). Figures *a*, *b*, *d*-*j*, modified after Lovén, 1892, pl. 9, figs. 93, 109, 101, and text fig. p. 73. Interambulacral plates stippled in figs. *e*-*j*.

(fig. 9, *a*, *b*, *d*, *h*-*j*) the auricles have migrated onto the basicoronal interambulacral plates and are fused together so that there are only five processes. The lantern is well developed and present in all members of the order but lacks the compass. The teeth are keeled (fig. 10) and are enameled at the tip. The pyramids are

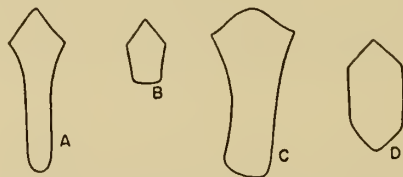


Fig. 10. Cross section of teeth of clypeasteroid echinoids (enlarged): *a*, *Echinarachnius parma* (Lamarek), after Lovén, 1892, pl. 10, fig. 135. *b*, *Hupea decagonalis* (Lesson), after Lovén, 1892, pl. 10, fig. 139. *c*, *Clypeaster reticulatus* (Linnaeus), after Lovén, 1892, pl. 10, fig. 131. *d*, *Helio-phora orbiculus* (Linnaeus), original.

widely expanded; the epiphyses and rotulae are small. In the flattened genera the lantern is likewise low.

GROWTH

The skeletal parts of the Echinodermata are of mesodermal origin and therefore are susceptible to much greater modification than those of organisms such as the mollusks and the arthropods, in which the hard parts are secreted by the ectoderm. In life, except for the tips of the spines in some of the regular echinoids, and the tips of the teeth, the hard parts are normally completely covered externally by a thin layer of ectoderm. All the hard parts, except possibly the teeth, are composed primarily of calcium carbonate deposited in the form of a spongy meshwork shaped into the various plates, spines, spicules, and so forth, that compose the skeleton. In life, all the pores and canaliculi of the hard parts are filled with mesodermal tissue. The presence of the tissue may be easily demonstrated by treating the test or spines of a modern echinoid with a concentrated solution of a liquid household bleach (usually sodium hypochlorite), such as "Clorox," which removes the tissues and leaves the hard parts with a very spongelike texture; or conversely, by decalcifying the test with a weak acid, leaving the soft tissues. Because of this intimate relationship with the secreting tissues, the hard parts are easily repaired when damaged, or are replaced (the spines, for example) when lost. Crystallographically, each of the plates, spines, and other units of the skeleton is a single crystal of calcite, with the principal optical axis normal to the surface of the plates (Jackson, 1912, p. 52). The hard parts have been considered to consist entirely of CaCO_3 ; but Clarke and Wheeler (1917, pp. 25-27) have recorded from 6 to 12 per cent of MgCO_3 and minor amounts of iron, aluminum, sulphate, and phosphate. From their analyses, the amount of CaCO_3 may vary from about 78 to 93 per cent.

Jackson (1912, p. 51) in his authoritative work has stated: "The individual plate of the test grows by a constant addition to the exterior and resorption of the interior, which latter is composed of open lattice-like or trabecular tissue. . . . Sectioning a sea-urchin plate, we find no trace of its earlier shape or character within, any more than we find the traces of a young femur within in sectioning the femur of an adult dog." Most, if not all, paleontologists and many zoologists have seemingly accepted this conclusion, although evidence to the contrary was published long ago. More than a century ago, M'Clelland (1841) in his paper on a new genus (*Cyrtoma*) incidentally described and figured growth lines in one of the living Indian echinoids. He made thin sections of plates that clearly showed concentric, alternating light and dark bands and interpreted them as growth rings. Since that date a few zoologists have made similar observations. Deutler (1926), in an extremely important paper that has been almost completely neglected by systematists and morphologists, gave much valuable data on the growth of the echinoid test, showed that many of the classic concepts are erroneous, presented numerous excellent figures of growth lines, and recorded their presence in various skeletal parts of some two dozen different species. Moore (1935) described and figured growth lines in the genital plates of *Echinus esculentus* from the coast of England. At the same time, he clearly indicated that the other plates of the test also show growth rings but that he had used the genital plates merely for convenience. He showed that the dark bands represent rapid summer growth and that the number

of annual rings agreed with the size groups in the local populations. Thus, in this species and therefore presumably in others, the growth rings are annual and are not related to lesser cycles. Moore also states that the spawning period occurs within the spring growing season of this species. He noted that most of the large individuals of *E. esculentus* were from four to six years old. Zoeke (1952) suggested that the growth rings in the clypeasters she reported upon probably represented sexual cycles. If *Clypeaster* has annual spawning habits like those of *E. esculentus*, then the specimen of *Clypeaster* figured by Zoeke (1952, fig. 5) was about twenty-five years old.

Growth rings have not been investigated in detail in the present study, but their presence has been observed in a number of genera and a preliminary notice has been published (Durham, 1951). Their presence has been noted in specimens of *Antillaster*, *Arbacia*, *Clypeaster*, *Conoclypeus*, *Dendraster*, *Echinarachnius*, *Encope*, *Mellita*, *Mellitella*, *Monostychia*, *Pericosmus*, *Scaphechinus*, *Scutellaster*, and *Strongylocentrotus*, both from tropical and from temperate zones. Some of the better examples are here illustrated (pls. 1 and 2). In accordance with Moore's observations (1935, p. 120) it was noted that not all specimens from a single locality clearly show growth lines, and that this percentage varies from locality to locality.

During the study of *Scutellaster interlineatus* it was observed that the growth lines are not strictly concentric but show changes in outline agreeing with the changes in shape of the plate as the test grows and new plates are added. The growth lines thus record the ontogeny of the individual plate and its changing relationships to other plates during that part of the life of the individual represented by the particular plate examined. The first post-basiceoral plates and the marginal aboral plates (pl. 3, figs. 5 and 6) show the greatest changes in shape. On the aboral surface the number of growth lines per plate decreases toward the apical system. It was also noted that smaller specimens had fewer growth lines in corresponding plates.

Preliminary studies indicate that growth lines are easily demonstrable in some species and difficult in others. In the genus *Scutellaster* (Pliocene, Pacific Coast), growth lines can easily be prepared for observation by the use of acids, or by removing the outermost surface and polishing. Many weathered specimens of this genus show well-defined growth lines. In the Recent *Dendraster excentricus*, the various techniques attempted were not very successful and growth lines could be demonstrated in only some specimens of a single population.

Assuming that all growth lines represent annual cycles, the approximate life span of the echinoids showing growth lines can be determined. Moore (1935, fig. 10) indicated that specimens of *Echinus esculentus* 8–10 cm. in diameter are five to seven years old. Zoeke's *Clypeaster*, about 18 cm. in diameter, was about twenty-five years old. A specimen of *Scutellaster interlineatus* (pl. 3, fig. 7) originally about 8 cm. long has about eight annual rings in marginal plates. A specimen of *Mellita quinquesperforata* 53.5 mm. long has three annual rings in marginal plates. Gordon (1929, p. 307) reported that at the end of four (winter) months young *Echinarachnius parma* had a test diameter of only 1 mm. This seems fully compatible with the age of about seven years inferred from the annual rings on

the oral surface of a specimen (pl. 4, fig. 4) of this species slightly more than 48 mm. long. Mortensen (1921, p. 102) has shown that northern individuals of *Dendraster excentricus* of a diameter of 55–70 mm. must be at least three years old, and that individuals 4 mm. in diameter represent the young “of the preceding summer.” The available data thus indicate that the larger echinoids may have a life span ranging from several years to perhaps twenty-five years.

The unbroken continuity of the growth lines in the coronal plates certainly indicates that no extensive resorption has affected them and probably indicates that none at all has occurred in them. The nuclear area of the plates with growth lines showing the outline of the early stages of the plates indicates, contrary to Jackson’s opinion, that no significant “addition to the exterior and resorption of the interior” has occurred, else the traces of the early developmental stages of the plates would have disappeared. From the available evidence it appears that, in those echinoids with growth lines, growth must take place concurrently over the entire inner and lateral surfaces of the plates, although at different rates at different places. The exterior of the plate is covered by a thin calcareous “epidermis,” and, except in the tubercles, additional growth does not seem to occur on this surface.

A good deal of interesting data is available on the addition of plates to the test. Gordon (1929, table 1, p. 309) has shown that in *Echinarachnius* three to six plates (depending on the area and stage of development) are present in each area at the time of metamorphosis, and that the periproct has assumed its adult position with respect to the plates of interambulacrum 5. She has also described (Gordon, 1926) a similar development for the spatangoid *Echinocardium*. From her investigations it is clear that the periproct does not change its position with respect to individual plates after those plates have started to form, although her studies show that occasionally the periproct may vary in position by having one more or one less plate between it and the peristome.

Examination (table 1) of fifty-two individuals of *Dendraster excentricus* from a single colony, ranging in size from an average diameter of 8.0 to 89.0 mm. shows several interesting facts. First, the number of plates on the oral surface in interambulacrum 5b and ambulacrum Ib is the same throughout this size range. Another series of six individuals (fig. 11) from a different locality, ranging in diameter from 4.4 to 18.6 mm., confirms this observation. Similarly, the plates on the aboral surface outside the petal, in ambulacrum Ib only, vary from 5 to 7 (one individual) in number—the twelve smallest individuals having 5 plates and the larger individuals usually 6 plates. This might be taken to indicate that, once the petals are formed, plates do not migrate from them. Inside the petals, the plates in the same column increase from 11 plates in the individual 8 mm. in diameter to 52 plates in an individual 89 mm. in average diameter (an average diameter of one-half length + width has been used in an attempt to obviate differences in proportions of different individuals). The number of plates does not always correspond to the size, a variation that might possibly be due to differences in food supply or some similar factor affecting total growth rate. It appears probable that the number of plates inside the petals is a better indication of the age than is the absolute size. On the aboral surface, the plates in interambulacrum 5b increase

TABLE 1
VARIATION IN NUMBER OF PLATES IN *Dendraster excentricus* (Eschscholtz)
FROM A SINGLE LOCALITY IN PUGET SOUND

Explanation of columns: I—Size ($\frac{1}{2}$ length + width); II—Number of post-basicoronal plates in interambulacrum 5b on oral surface; III—Number of plates in interambulacrum 5b on aboral surface; IV—Number of post-basicoronal plates in ambulacrum Ib on oral surface; V—Number of plates in ambulacrum Ib on aboral surface outside petal; VI—Number of plates inside petal in ambulacrum Ib.

I	II	III	IV	V	VI
89	3	10	5	6	51
89	3	11	5	6	52
88	3	10	5	7	50
85	3	11	5	6	48
80	3	9	5	6	45
78	3	10	5	6	46
77.5	3	10	5	6	48
77.5	3	8	5	6	50
73.5	3	10	5	6	45
73	3	9	5	5	50
70	3	9	5	6	36
69	3	9	5	6	42
68	3	8	5	5	44
67.5	3	9	5	6	44
66.5	3	8	5	6	42
66.5	3	9	5	6	44
66	3	9	5	6	39
60	3	9	5	6	46
58.5	3	9	5	6	41
54	3	10	5	6	42
53	3	8	5	6	36
47.5	3	10	5	6	33
44.5	3	10	5	6	37
40	3	9	5	6	34
37	3	9	5	6	28
35	3	9	5	6	31
33.5	3	8	5	5	30
33	3	9	5	6	32
32.5	3	9	5	6	31
31.5	3	8	5	6	25
29.5	3	8	5	6	24
28	3	8	5	6	24
27	3	8	5	5	24
25.5	3	8	5	6	22
24.5	3	8	5	5	21
23.5	3	8	5	6	24
21.5	3	8	5	5	21
20	3	7	5	6	19
19	3	8	5	6	18
17.5	3	8	5	6	17
15.5	3	8	5	5	19
15.3	3	7	5	5	16
15	3	8	5	5	18
14.1	3	8	5	5	17
13.2	3	7	5	5	13
12.9	3	7	5	5	14
11	3	7	5	5	13
10.9	3	7	5	5	13
10.5	3	7	5	5	12
9.7	3	7	5	5	12
9.2	3	6 (?)	5	5	11
8.0	3	6 (?)	5	5	11

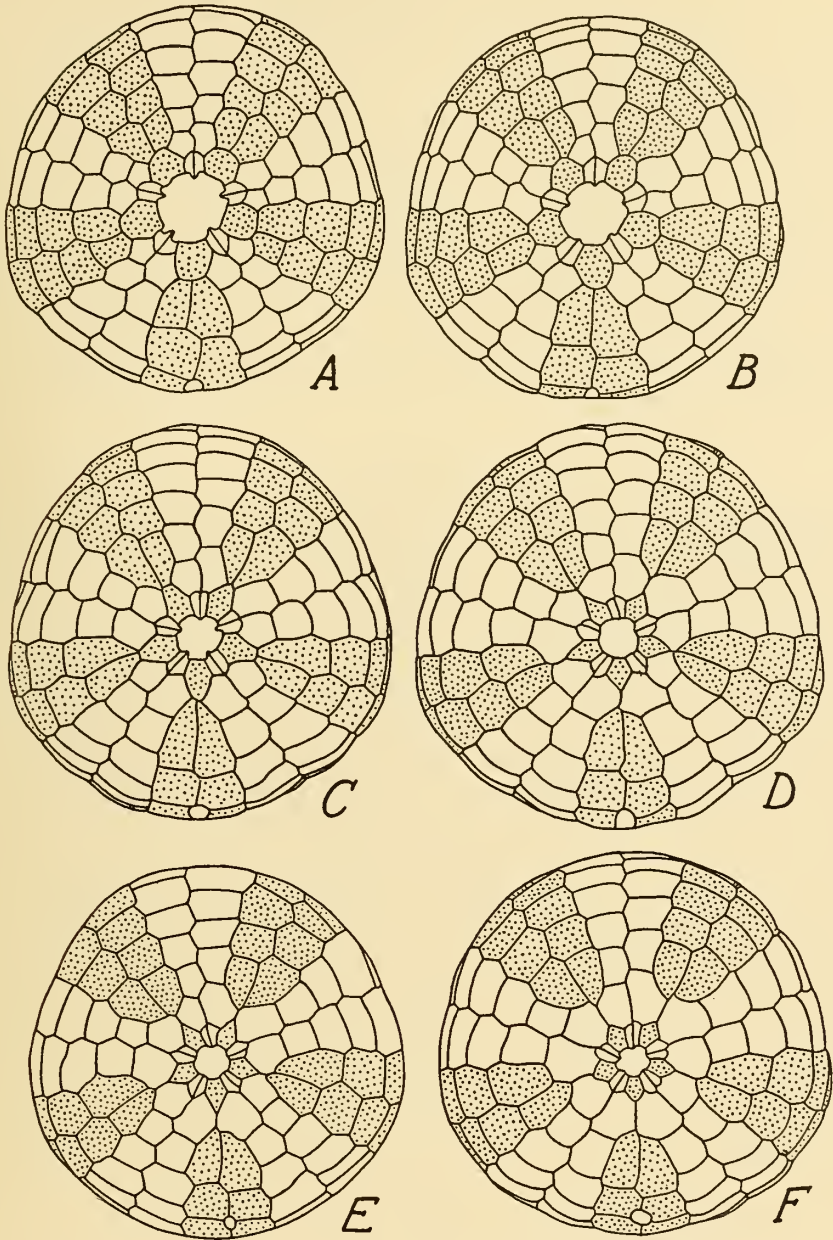


Fig. 11. Ontogeny of oral surface of *Dendraster excentricus* (Eschscholtz); Recent, Tomales Bay, California. Figs. a-f, respectively, after hypotypes nos. 33793, $\times 12.6$; 33794, $\times 8.3$; 33797, $\times 5.9$; 33798, $\times 4.4$; 33799, $\times 2.8$; 33800, $\times 2.4$.

from 7 in the individual 9.7 mm. in diameter to 11 in the individual with the maximum number of plates in the petal. Like the plates in the petals, they do not increase in number consistently with increase in size. It is apparent that, except for the area within the petals, growth in *Dendraster* takes place primarily by

increase in size of plates rather than by addition of new plates. It would seem that most of the plates, except those in the petals, are formed by the time of metamorphosis or immediately thereafter.

Studies (table 2) of one hundred adult (average diameter 50 to 62 mm.) specimens of *Echinarachnius parma* from a single locality in general confirm the observations on *Dendraster*. The number of plates in any column on the oral surface, except in three individuals, varies by only one plate. Because sutures next to the ambitus are often extremely difficult to recognize or prepare, the number of variants recorded may be larger than the real number; but since sutures have been clearly recognized in a few specimens, it is evident that there is some variation in the number of plates. However, the additional plates present or absent are always those bordering on the ambitus. On the aboral surface the variations observed are similar to those in *Dendraster*.

STRUCTURE

In all clypeasteroid echinoids the test is primitively composed of 20 columns of plates extending from the basicoronal plates around the peristome to the oculo-genital ring. These 20 columns are combined into 5 ambulacral and 5 interambulacral areas of 2 columns each. In the adults of some of the advanced genera (for instance, *Dendraster*, fig. 11, *f*), some or all of the interambulacral columns may be separated from the single basicoronal interambulacral plate by the junction of the enlarged, adjacent, immediate post-basicoronal ambulacral plates. Adapically, next to the genital plates, the 2 interambulacral columns are reduced to 1 in the rotulid, laganid, neolaganid, and fibulariid genera (for instance, *Rotula*, fig. 12, *c*, and *Laganum*, fig. 12, *b*). On the oral surface the ambulacral columns consist of relatively few plates and are as wide as or wider than the adjacent interambulacral columns, a characteristic which gives unity to the group and differentiates them from all other irregular echinoids. On the apical surface a part of the ambulacral area is formed into more or less well-defined petals. Among the more specialized genera, there may be a large number of small plates within the petals, but in the primitive genera, such as *Scutellina*, with more or less open petals, these plates may be few and relatively large. In the families Clypeasteridae, Arachnoididae, and Neolaganidae, the plates within the petals are usually "compound"; but in the other families the ambulacral plates are all simple.

In the Clypeasteridae, Arachnoididae, and Neolaganidae, associations of primary, demi-, and occasionally occluded plates occur in the petaloid parts of the ambulacra, at times closely resembling the combinations of plates present in compound plates in the sense of Hawkins (1920, pp. 394-398). In the Clypeasteridae and Arachnoididae, so far as now known, the primary and demiplates (fig. 12, *a*) are never bound together by large, overlapping primary tubercles. In these two families the tubercles are always smaller than the individual plates and are not known to cross sutures. Seemingly, these plates are not compound in the sense of Hawkins. In the Neolaganidae complex sequences of primary, demi-, and occluded plates may occur (fig. 27, *a-c*). Here the primary tubercles within the petals are often large and may rest on two or three plates in a single column, or, in species in which the interporiferous area is narrow (e.g., *Sanchezella sanchezi*),

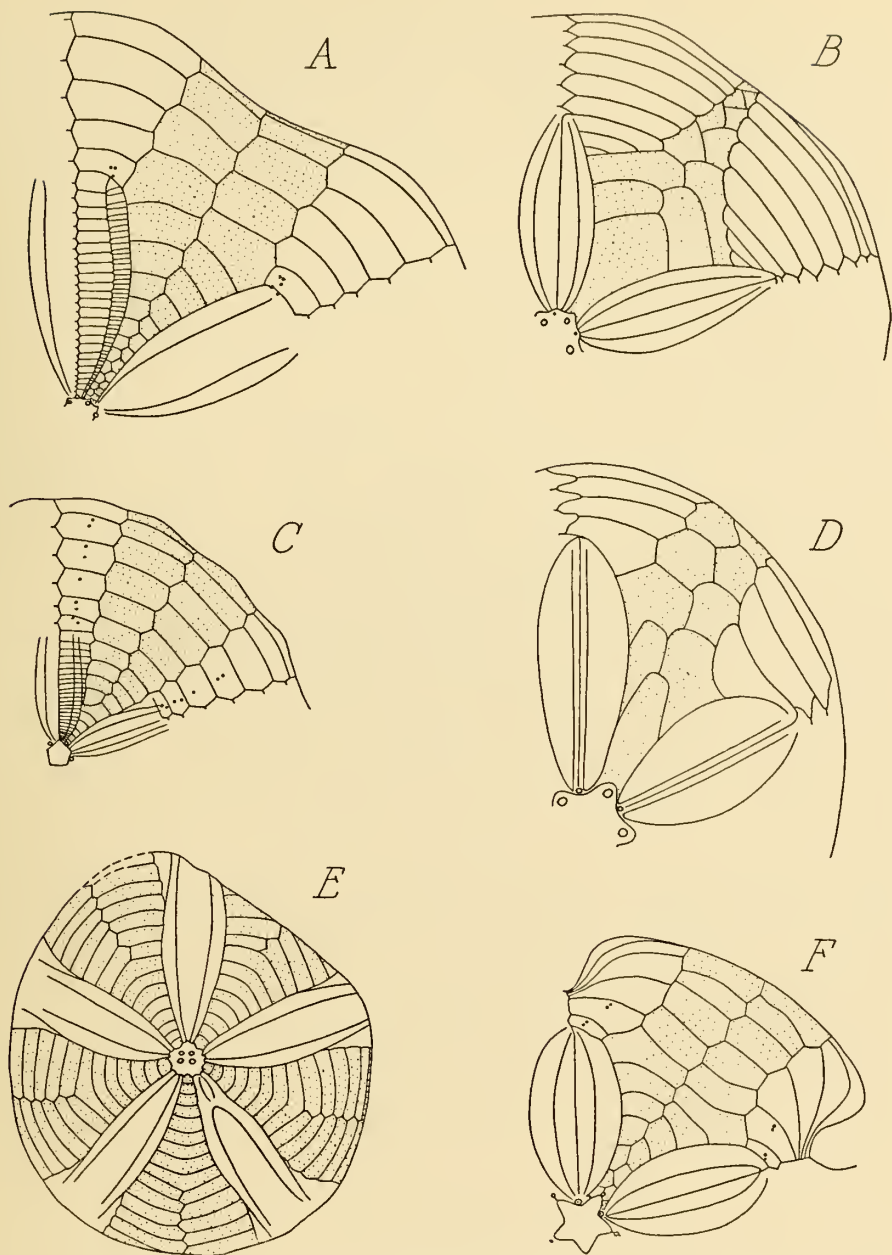


Fig. 12. Apical termination of clypeasteroid interambulaera: *a*, *Clypeaster ravenelii* (A. Agassiz), $\times 0.8$, after hypotype no. 33381; Recent, Gulf of Mexico. *b*, *Laganum laganum* (Leske), $\times 1.6$, after hypotype no. 33258; Recent, New Hebrides. *c*, *Heliophora orbiculus* (Linnaeus), $\times 1.68$, after hypotype no. 33816; Recent, Loanda, Angola. *d*, *Sanchezella sanchezi* (Lambert), $\times 1.88$, after hypotype no. 33260; upper Eocene, Cuba. *e*, *Tarphypygus clarki* (Lambert), after Paleont. Res. Inst. hypotype no. 20513; upper Eocene, Cuba. *f*, *Encope grandis* L. Agassiz, $\times 1.5$, after hypotype no. 33809; Recent, Gulf of California.

the tubercle may straddle the perradial suture and rest on two plates in each column. Whether or not any of those grouped plates are bound together in the manner specified by Hawkins (1920, p. 395) has not been determined as yet. Accordingly, the term "compound" is loosely used in this paper to describe the occurrence of demi- and occluded plates in the petaloid areas of the ambulacra, with the realization that some, at least, of these associations are not truly compound in the sense of Hawkins.

The apical system is composed of a single large plate, the madreporite, and five smaller plates, the oculars, that are not always clearly separable from the madreporite. Mortensen (1948, p. 1) and most earlier workers have stated that the separate genital plates of the regular echinoids are all fused with the madreporite in the irregular echinoids. However, Gordon (1929, p. 321) has shown that in *Echinarachnius*, and therefore presumably in other clypeasteroids, genital plates 1 and 3 are completely lost at the time of metamorphosis, genital plate 5 never develops, and only genitals 2 and 4 fuse to form the madreporite. She further emphasizes that this is the only echinoid in which she has observed fusion of plates. Gordon did not observe the development of the genital pores in any of the specimens of *Echinarachnius* that she studied, and they have not yet appeared in specimens 9.5 mm. in diameter. In young *Dendraster excentricus* from Puget Sound, the genital pores first appear in individuals between 12 and 15 mm. in length. In *Heliphora orbiculus* they appear at a similar size. Genital pores have been reported in the much smaller species *Peronella peronii* at a diameter of 5 mm. (Mortensen, 1948, p. 262). The genital pores are usually situated within the expanded madreporite, but in *P. peronii* they occur outside the madreporite in the interambulacra (Mortensen, 1948, p. 262). Most genera have only four genital pores, but some genera (*Clypeaster*, *Laganum*, *Hupea*, *Jacksonaster*, *Protoscutella*, *Periarchus*, *Mortonella*, *Encope*, and *Mellitella*) have five. In most of the clypeasteroids the madreporite is more or less pentagonal, and the apices of the pentagon correspond to the interambulacra; sometimes it may be modified into an irregular pentamerous star, as in *Peronella lesueuri* (Mortensen, 1948, fig. 159), with the points extending out into the interambulacra. However, in the rotulids the apices of the pentagon correspond to the ambulacral areas, and the genital pores are situated in reëntnants on the sides. The hydropores begin to appear before metamorphosis is complete (Gordon, 1929, fig. 19) and apparently may increase in number as growth proceeds. In many genera they are apparently dispersed irregularly throughout the madreporite, but in the laganids and neolaganids they may open into an irregular groove (Mortensen, 1948, p. 242, fig. 157). Only Mortensen has given much attention to this groove, yet the present studies would indicate that it is of considerable significance at the generic level. It is present in the type species of *Sismondia* (Eocene of France), the Eocene and Oligocene neolaganids of the New World, and many of the later Cenozoic laganids of the Indo-Pacific. In *Cubanaster torrei*, the detailed branching of the groove (fig. 13) varies in different individuals, but a branching groove is present in all individuals (more than twenty-five) examined.

Around the peristome are the 15 basicoronal (Jackson, 1912, pp. 69-73), or primordial, plates: 10 ambulacral and 5 interambulacral (figs. 14-16). Jackson

states that these are the first-formed plates of the corona, and it appears probable that they were developed nearly concurrently with the oculogenital plates. Gordon (1926, 1929) has shown that by the time metamorphosis is complete in the two irregular echinoids she studied, several plates are present in each ambulacral and interambulacral column, and that the new plates are added adapically next to the oculogenital plates; the basicoronal plates are therefore the oldest plates of the test outside the apical system. The present studies have shown that in the primitive clypeasteroids (e.g., *Echinocyamus*, fig. 14, *a*) the basicoronal plates are relatively undifferentiated. In the specialized genera either the ambulacral (e.g., *Clypeaster*, fig. 15, *a* and *b*) or the interambulacral (e.g., *Amphiope*, fig. 16, *d*; or *Eoscutella*, fig. 16, *f*) plates may become greatly enlarged at the expense of the others.

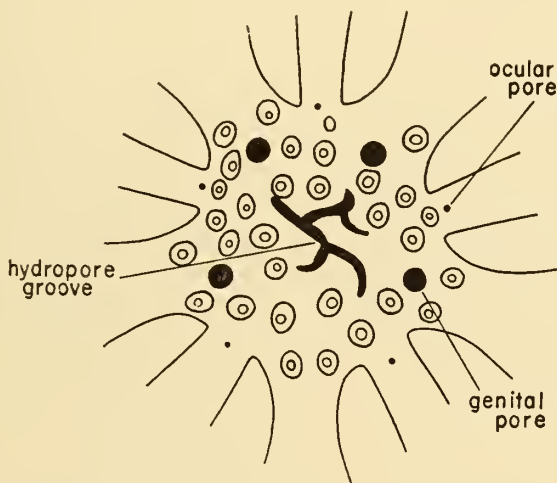


Fig. 13. Hydropore groove of *Cubanaster torrei* (Lambert), $\times 17.5$, diagrammatic after hypotype no. 33299; upper Eocene, Panama.

Among the scutellinid echinoids the geologically younger genera (e.g., *Encope*, fig. 17, *c* and *d*) tend to have the interambulacral columns separated from the basicoronal plates, whereas in the older genera (e.g., *Scutella*, fig. 18, *a*, and *Periarchus* fig. 18, *c*), these columns and plates are in contact. This separation may not occur concurrently in all areas. Most of the Recent genera of this group have the columns separated, but all the early Tertiary genera have the columns in contact with the basicoronal plate.

Among the rotulinids an extremely unusual condition (fig. 19) occurs in the basicoronal row. In the adult, 20 instead of 15 plates are present, the additional 5 plates being interambulacral. Although the smallest individual available for examination was 10 mm. in diameter, a study of a sequence (fig. 19, *a-c, g*) from this size up to fully adult individuals seems to indicate that this represents an ontogenetic process whereby post-basicoronal plates are pushed into the basicoronal row. From the small amount of available material it is impossible to ascertain from which column the extra plates are derived. In *Rotula decicsdigitata* (fig. 19, *d*) 2 of the basicoronal interambulacral plates (in areas 1 and 4) are

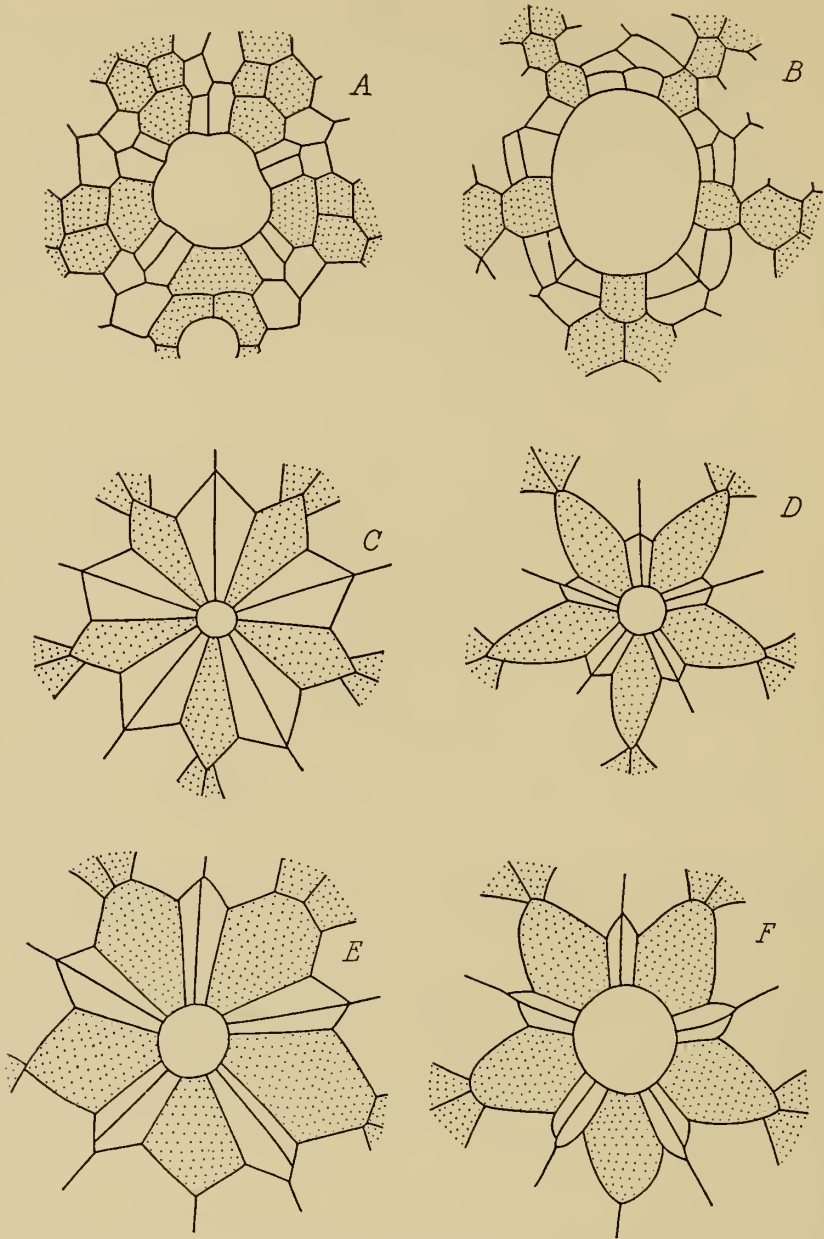


Fig. 14. Clypeasteroid basicoronal plates: *a*, *Echinocyamus pusillus* (Müller), enlarged, after Lovén, 1874, pl. 44, fig. 235. *b*, *Tarphypygus clarki* (Lambert), $\times 11.6$, after Paleont. Res. Inst. hypotype no. 20512; upper Eocene, Cuba. *c*, *Scutella subrotunda* (Leske), $\times 1.6$, after specimen no. E 2328 British Museum (Natural History); "Oligo-Miocene," Malta. *d*, *Periarchus lyelli pileus-sinensis* (Ravenel), $\times 2$, after hypotype no. 33830; upper Eocene, Georgia. *e*, *Remondella gabbii* (Rémond), $\times 6.4$, after hypotype no. 33401; upper Miocene, California. *f*, *Astrodapsis brewerianus* (Rémond), $\times 6$, after hypotype no. 11016; upper Miocene, California.

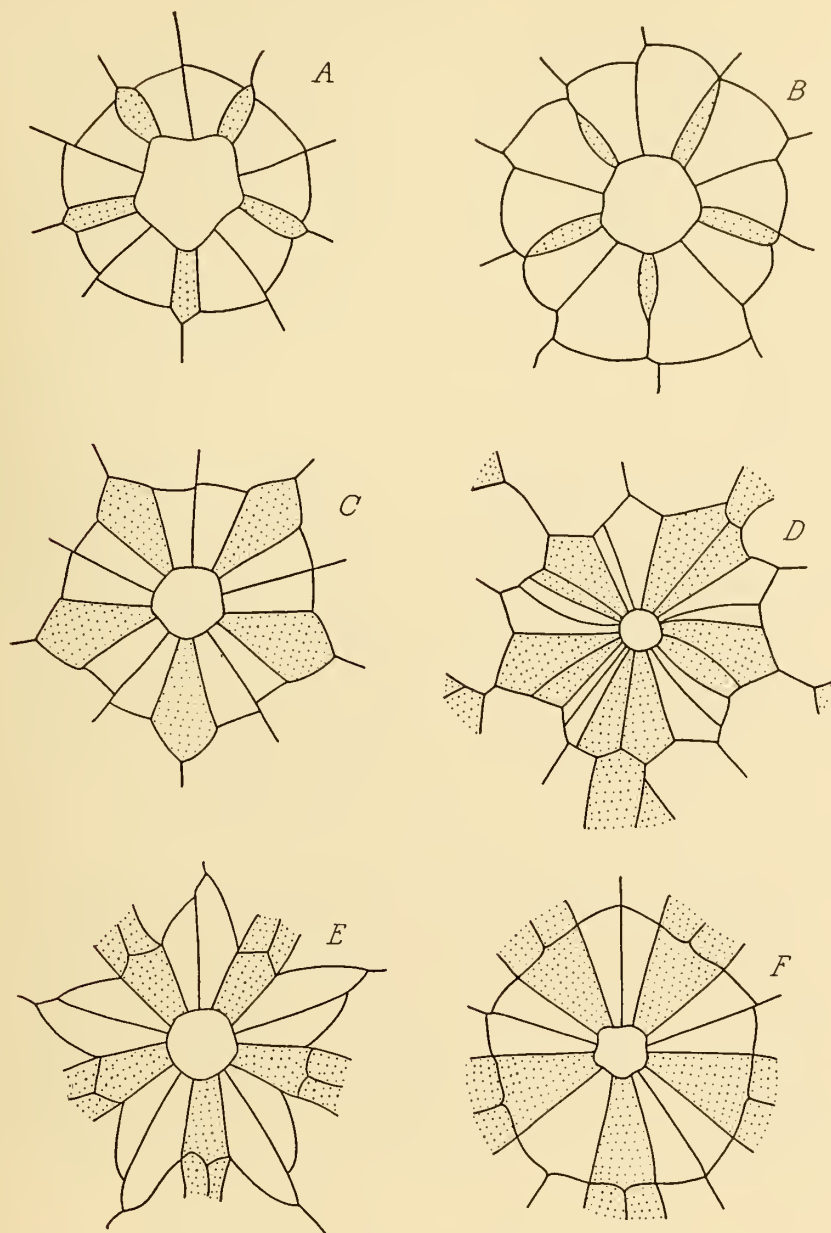


Fig. 15. Clypeasteroid basicoronal plates: *a*, *Clypeaster rosaceus* (Linnaeus), $\times 1.2$, after hypotype no. 33372; Recent, Florida. *b*, *Clypeaster reticulatus* (Linnaeus), $\times 4$, after hypotype no. 33373; Recent, Philippine Islands. *c*, *Arachnoides placenta* (Linnaeus), $\times 2.4$, after hypotype no. 33351; Recent, east coast of Sumatra. *d*, *Heliophora orbiculus* (Linnaeus), $\times 3.6$, after hypotype no. 33815; Recent, Loanda, Angola. *e*, *Laganum laganum* (Leske), $\times 2.8$, after hypotype no. 33259; Recent, New Hebrides. *f*, *Neolaganum archerensis* (Twitchell), $\times 3.8$, after hypotype no. 33296, upper Eocene, Florida.

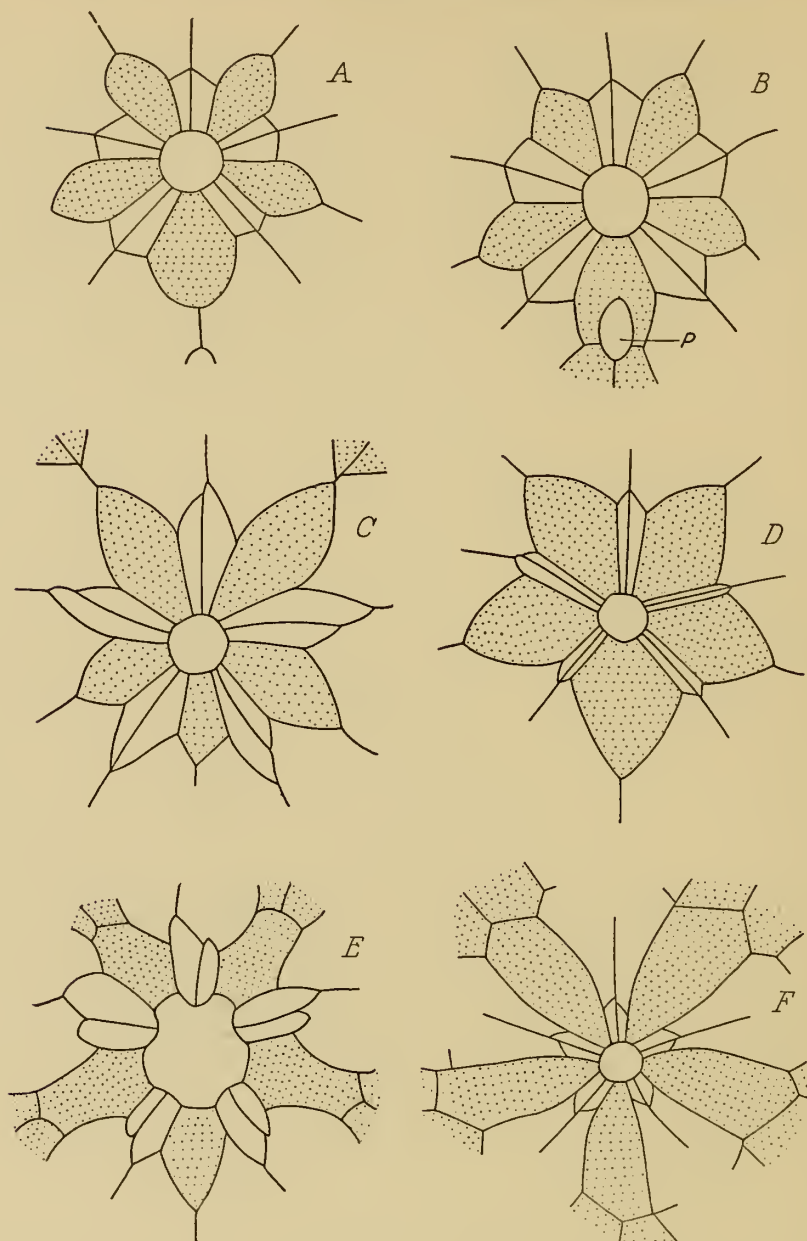


Fig. 16. Clypeasteroid basicoronal plates: *a*, *Encope emarginata* (Leske), $\times 2.4$, after hypotype no. 33792; Recent, Gulf of Mexico. *b*, *Mellita quinquiesperforata* (Leske), $\times 4.8$, after hypotype no. 33802; Recent, Gulf of Mexico. *c*, *Vaquerosella vaquerosensis* (Kew), $\times 2.4$, after "cotype" no. 11403; lower Miocene, California. *d*, *Amphiope bioculata* (Des Moulins), $\times 3.6$, after hypotype no. 33846; Miocene, Europe. *e*, *Pseudoastrodapsis nipponicus* (Nisiyama), $\times 6.4$, after paratype no. 30131; "Mio-Pliocene," Japan. *f*, *Eoscutella coosensis* (Kew), $\times 2.8$, composite after hypotype nos. 33386 and 33387; upper Eocene, Oregon.

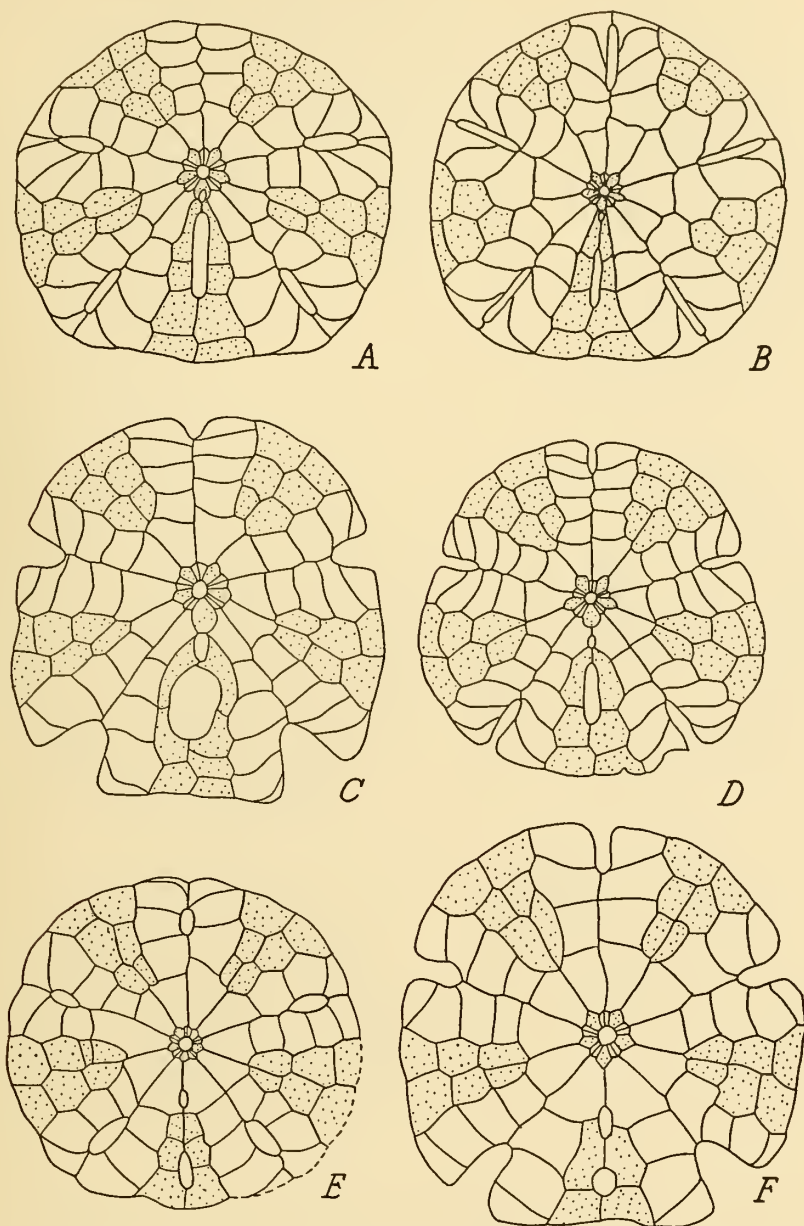


Fig. 17. Structure of oral surface of clypeasteroid echinoids: *a*, *Mellita quinquiesperforata* (Leske), $\times 0.85$, oral view, hypotype no. 33802; Recent, Gulf of Mexico. *b*, *Leodia sexiesperforata* (Leske), $\times 0.57$, oral view, hypotype no. 33384; Recent, east coast of United States. *c*, *Encope grandis* L. Agassiz, $\times 0.64$, oral view, hypotype no. 33809, basicoronal plates in part after specimen no. 33810; Recent, Gulf of California. *d*, *Encope emarginata* (Leske), $\times 0.78$, hypotype no. 33792; Recent, Gulf of Mexico. *e*, *Mellitella angelensis* (Durham), $\times 0.9$, oral view, paratype no. 14962, margin restored in part; Pliocene, Gulf of California. *f*, *Mellitella* sp., $\times 1.2$, oral view, hypotype no. 33806; Miocene, Venezuela.

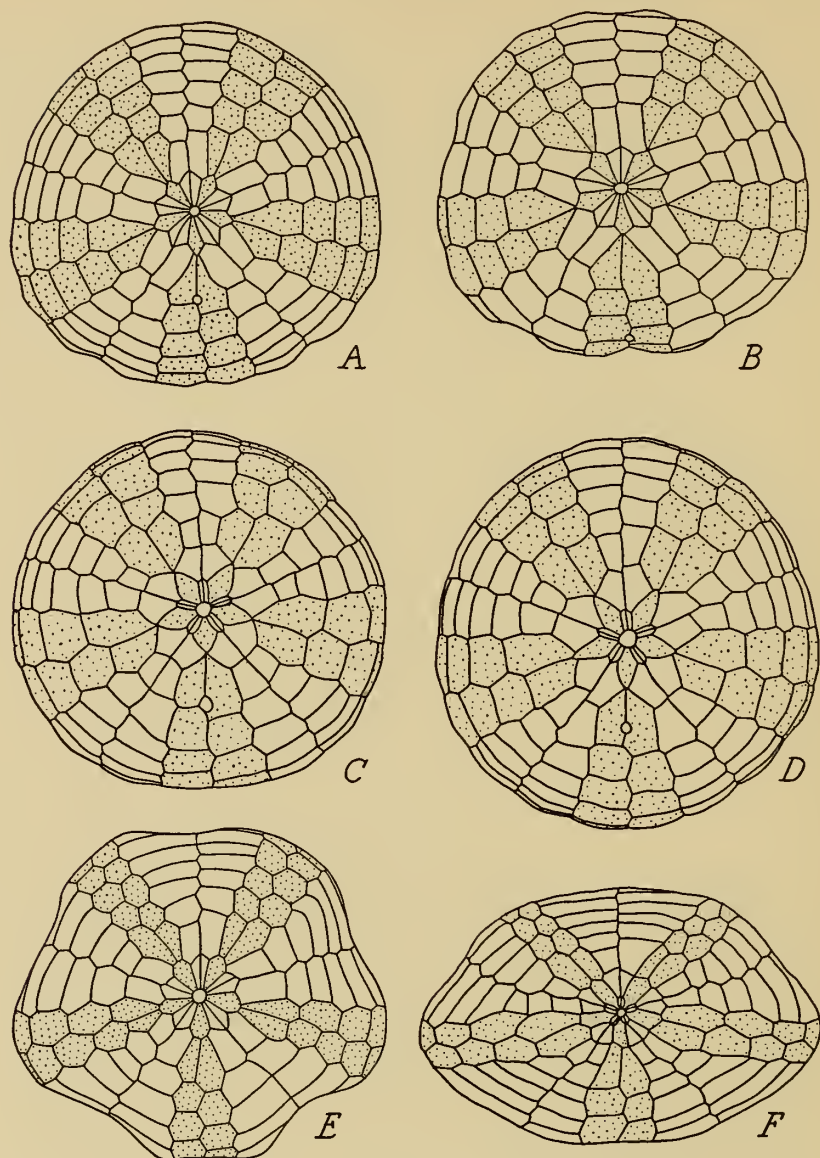


Fig. 18. Structure of oral surface of clypeasteroid echinoids: *a*, *Scutella subrotunda* (Leske), $\times 0.45$, oral view, topotype, British Museum (Natural History) no. E 2328; "Oligo-Miocene," Malta. *b*, *Parascutella leognanensis* (Lambert), $\times 0.47$, oral view, after L. Agassiz, 1841, pl. 17, fig. 2; Burdigalian, France. *c*, *Mortonella quinquefaria* (Say), $\times 0.8$, oral view, hypotype no. 33841; upper Eocene, Georgia. *d*, *Periarchus lyelli pileus-sinensis* (Ravenel), $\times 0.8$, hypotype no. 33830; upper Eocene, Georgia. *e*, *Parmulechinus subtetragona* (Grateloup), $\times 0.85$, oral view, diagrammatic after British Museum (Natural History) specimens E 41480 and E 41481; Tongrian, France. *f*, *Eoscutella coosensis* (Kew), $\times 0.68$, oral view, after hypotypes nos. 33386 and 33387, partly restored; upper Eocene, Oregon.

much reduced in size and at times are difficult to observe. In *Rotuloidea* (fig. 19, *f*) and *Heliophora* (fig. 19, *g*) this reduction is not so marked although it is still apparent. Lovén (1874, pl. 46, fig. 238) does not show this condition in his figure

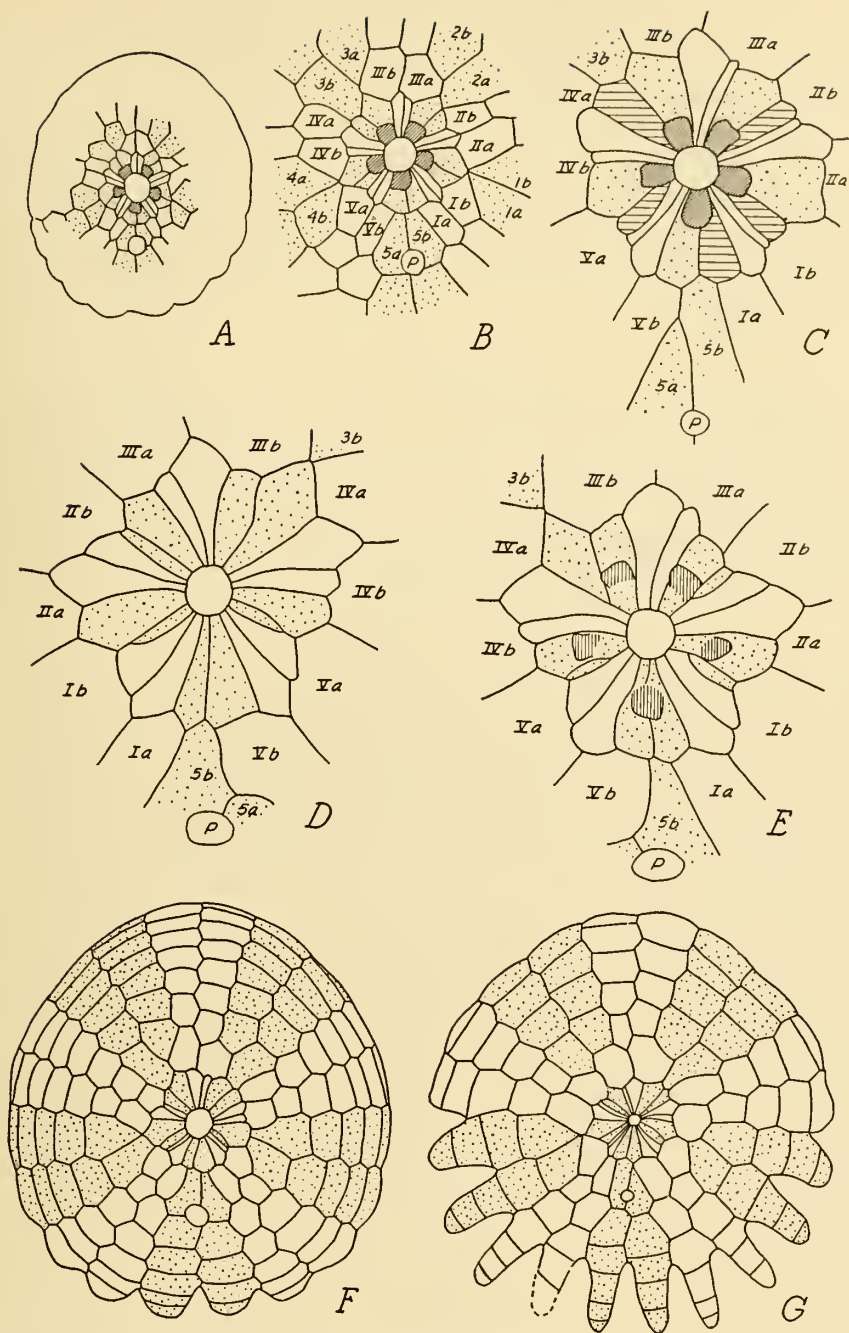


Fig. 19. Structure of oral surface of clypeasteroid echinoids: *a*, *Heliophora orbiculus* (Linnaeus), $\times 3.4$, internal view of plates around peristome with outline of test, hypotype no. 33812; young individual, auricles shaded; Recent, Loanda, Angola. *b*, *Heliophora orbiculus* (Linnaeus), $\times 3.4$, internal view, with position of periproct (P) indicated, hypotype no. 33813; young, auricles shaded; Recent, Loanda, Angola. *c*, *Heliophora orbiculus* (Linnaeus), $\times 4.4$, internal view, with position of periproct (P) indicated, hypotype no. 33815; adult, auricles shaded; Recent, Loanda, Angola. *d*, *Rotula deciesdigitata* (Leske), $\times 3.4$, oral view, with position of periproct (P) indicated, hypotype no. 33853; adult; Recent, Loanda, Angola. *e*, *Rotula deciesdigitata* (Leske), $\times 3.4$, internal view, with position of periproct (P) indicated, same specimen as *d*, auricles shaded. *f*, *Rotuloidea fimbriata* Etheridge, $\times 1.4$, oral view, hypotype no. 33300; Pliocene, Morocco. *g*, *Heliophora orbiculus* (Linnaeus), $\times 1.28$, oral view, same specimen as *c*; Recent, Loanda, Angola.

of *Heliophora*, but it is present in all specimens (more than twenty-five of *Heliophora*) of the three genera examined.

In an ontogenetic series (fig. 11) of *Dendraster excentricus* the very young stages have basicoronal plates somewhat similar to those of the primitive clypeasteroids, proportionally very large, and in contact with the post-basicoronal plates in the interambulacra. As the individuals increase in size, the basicoronal plates begin to assume the adult characteristics, become proportionally smaller, and become separated from the post-basicoronal plates in the interambulacral areas.

VARIATION IN STRUCTURE

During the survey of the clypeasteroid echinoids it was readily apparent that there are marked differences in the arrangement of the plates on the oral surface of specimens representing different genera and families, even though in general morphology they may be rather similar. In evaluating the significance of these differences, a special study was made of the genera *Dendraster* and *Astrodapsis*, as well as the species *Echinarachnius parma*.

The Genus *Dendraster*

Several thousand specimens of the common Recent *Dendraster* from the Pacific Coast, conventionally referred to *D. excentricus*, have been available for examination. They were collected at various localities from Puget Sound to Lower California and represent almost the entire geographic range of the genus. Different localities are represented by varying numbers of individuals, from a few to five hundred or more. Several hundred adult specimens, including two lots of about one hundred from single localities, were examined in detail, and many more were casually inspected for variation.

During preparation of the various specimens it was noted that it is more than usually difficult to prepare the area immediately adjacent to and on the ambitus so that the plates there could be differentiated. Since the plates in this region have very little altitude in comparison to their width, the precise number of plates present in this area in some specimens is rather uncertain. And since the number of plates in other areas of the test is constant in adults (barring obvious abnormalities), any apparent variation in number of plates present on, or immediately adjacent to, the ambitus of most flattened, scutelliform echinoids should be suspect, for it could have resulted from inadequate preparation of the specimens.

The study of the Recent individuals of *D. excentricus* has shown, barring abnormalities or the apparent variation discussed in the preceding paragraph, that the number of plates in the various columns on the oral surface is very constant (table 1) in all sizes of individuals, from those with an approximate diameter of 6 mm. (fig. 11) to the largest adults examined (about 90 mm. length). Great variation exists in the ambital outline of mature individuals from a single locality (fig. 20) and in the characteristic shape of individuals from different areas (some doubt exists whether the specimens from different localities represent the same species or subspecies). This variation ranges from differences in relative width versus length to changes in degree of rounding or angularity of ambital outline,

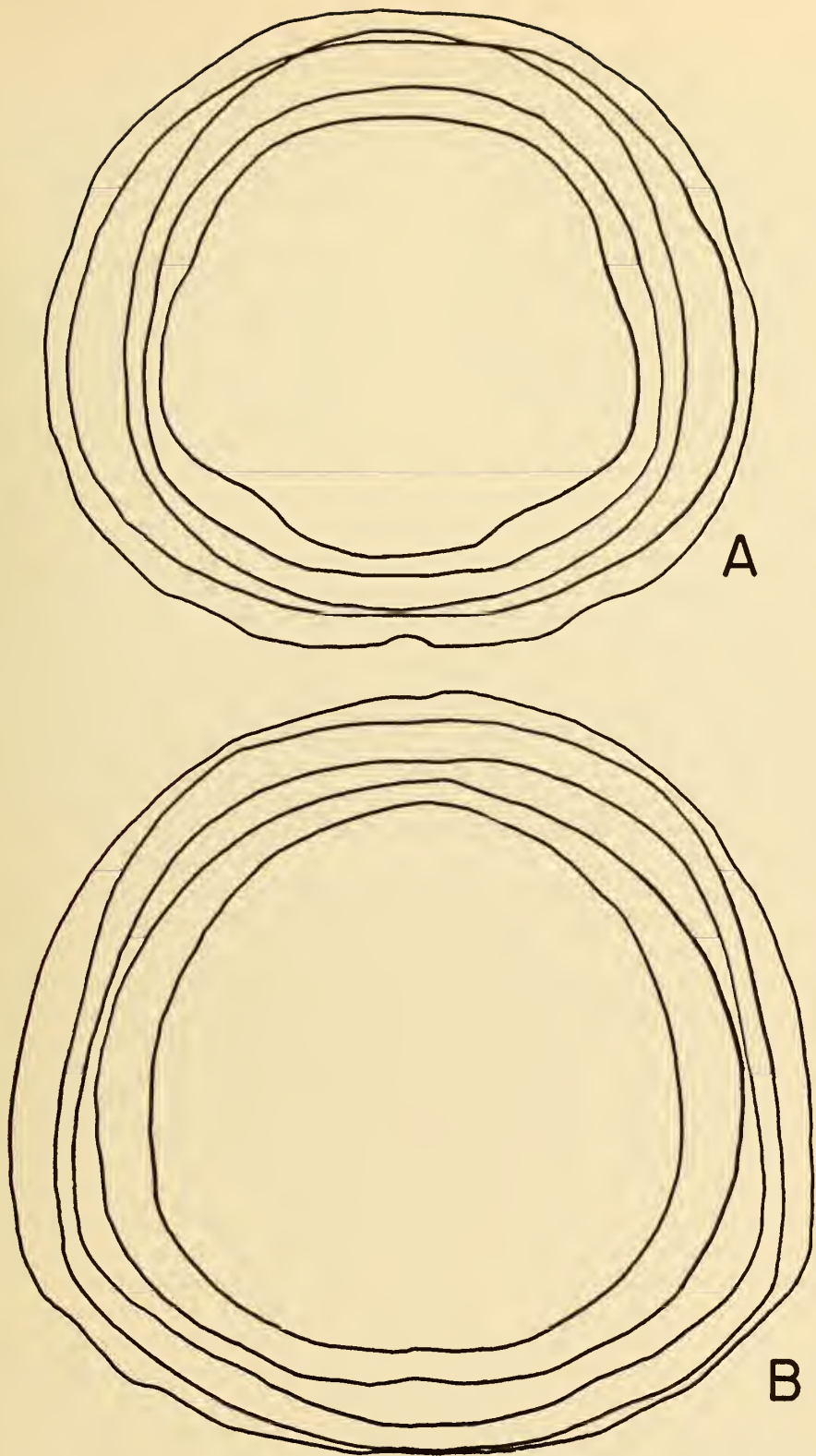


Fig. 20. Variation in outline of *Dendraster excentricus* (Eschscholtz): a, outline of typical specimens from various localities from Puget Sound to Lower California; oral view, about natural size. b, Variation in outline of specimens from an area of about 25 square feet in Bremerton Inlet, Puget Sound; oral view; outermost specimen about natural size, innermost reduced.

each of the variants being independent of the other. These variations in shape affect the outline of the individual plates of the oral surface; for the plates, being constant in number, adjust their shape to that of the test. Thus, individually, corresponding plates in different specimens may have varying shapes, although the differences are usually minor.

The plates of the oral surface have a characteristic adult arrangement, although occasional individuals have plates that have changed, as it were, from "right-handed" to "left-handed," the relative proportions being reversed in adjacent plates. It is normal for adult individuals (fig. 21, *a* and *b*) to have a circle of small primordial plates—10 ambulacrals and 5 interambulacrals—forming the *basicoronal* row around the peristome. Next outside the basicoronal plates is a row composed of 10 large ambulacral plates, which have enlarged so that they meet the corresponding plates of the adjacent ambulacrum and thus separate the second plates of the interambulacral areas from the basicoronal plates. This separation is present in about four hundred specimens—including lots from single localities of 81, 97, and 100 specimens each—that have been examined. In only one instance (interambulacrum 5) was there any tendency toward closure of the separation, and in this the gap was reduced only to one-half its normal size. Outside the row composed of ambulacral plates only, there appears to be a constant number of plates in each column in adult individuals. In all the individuals of this species that were carefully examined, except a few in which obvious abnormalities exist, the number of plates has been constant, even though there are great variations in shape to which the plates must adjust their outline. Even in young individuals of slightly less than 5 mm. diameter, this same number of plates is already present (fig. 11, *a*), although the relationships and proportions of the plates are markedly different.

Ontogenetic studies (fig. 11) show that the adult complement of plates for the oral surface is already present at a diameter of 4.4 mm. Thereafter, the plates grow differentially, causing a rearrangement as growth proceeds. In the very young individual noted above, the periproct is on the ambitus, and the basicoronal interambulacral plates are in full contact with the succeeding plates and are much larger than the adjacent basicoronal ambulacral plates. Except for the position of the periproct, there is considerable resemblance to the condition found in the type species of *Periarchus*, and at a diameter of 9.4 mm. (fig. 11, *c*) the resemblance (except for position of the periproct) is very close. As growth proceeds, the second plate of each ambulacral column grows faster than the others and eventually separates the second interambulacral plate from contact with the basicoronal interambulacral plate. Meanwhile, the basicoronal ambulacral plates grow faster than the basicoronal interambulacral plates, and by the time the adult size is reached they are nearly equal in size. The periproct slowly migrates from a position on the ambitus to its normal submarginal location. Stewart (Woodring, Stewart, and Richards, 1940, p. 81) has noted that in some specimens of *Dendraster coalingensis*—a species in which the periproct is usually submarginal—the periproct may be marginal or even supramarginal, indicating that migration to the "normal" submarginal position is not an invariable feature. However, in the several thousand available adult specimens nominally referred to *D. excentricus*, no adult with a marginal or supramarginal periproct has been noted.

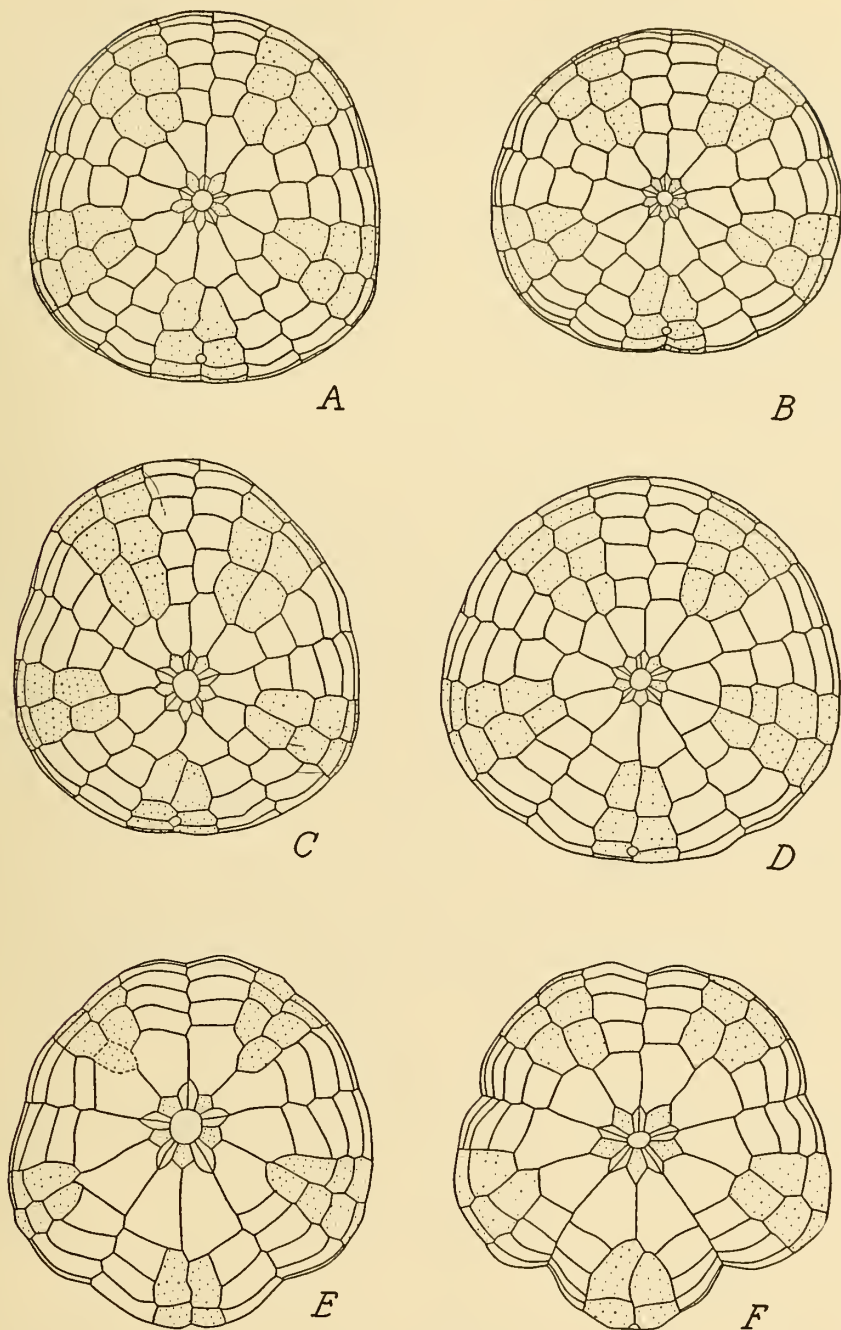


Fig. 21. Structure of oral surface of clypeasteroid echinoids: *a*, *Dendraster excentricus* (Eschscholtz), $\times 0.65$, oral view of an elongate individual, hypotype no. 33864; Recent, Puget Sound. *b*, *D. excentricus* (Eschscholtz), $\times 0.57$, oral view of rounded specimen from same colony as figure *a*, hypotype no. 33856; Recent, Puget Sound. *c*, *D. gibbsii* (Rémond), $\times 1.4$, oral view (extreme margin restored), hypotype no. 32941 (same specimen as text fig. 2, *c*, Durham, 1949); Pliocene, California. *d*, *D. laevis* H. L. Clark, $\times 1.14$, oral view, hypotype no. 33337; Recent, California. *e*, *Vaquerosella andersoni* (Twitchell), $\times 1.8$, oral view, hypotype no. 11363; lower Miocene, California. *f*, *Vaquerosella norrisi* (Pack), $\times 1.85$, oral view, holotype no. 11028; lower Miocene, California.

Even in the smallest specimens of *D. excentricus* examined, the periproct has been found to be approximately at the junction of the sutures between the second and third post-basicoronal plates of interambulacrum 5. The periproct may vary in position about half the height of one of these plates from the intersection of these sutures with the interr radial suture, usually moving closer toward the peristome.

According to Lovén's law, the basicoronal ambulacral plates Ia, IIa, IIIb, IVa, and Vb should always be larger than plates Ib, IIb, IIIa, IVb, and Va. This is usually but not invariably true in *D. excentricus*. Occasionally in some areas the plates are equal in size, in others the relationships are reversed, although they may not be reversed in all areas. Lovén's law is also expressed in the first post-basicoronal ambulacral plates, and here it is much more constant in its expression; but even so, occasional variants are found.

In addition to *D. excentricus*, specimens of *D. coalingensis* Twitchell, *D. elsmerensis* Durham, *D. gibbsii* (Rémond), *D. granti* Durham, and *D. laevis* H. L. Clark—all species which are clearly distinct from one another—were examined for variation of the arrangement of the plates on the oral surface at a specific level. In *D. gibbsii* (fig. 21, c), the species which is most eccentric and usually more elongated than any other member of the genus, the same number of plates is present on the oral surface. The elongation is achieved by elongation of individual plates and not by the addition of new plates. In *D. elsmerensis*, the most primitive member of the genus as judged by the normal marginal position of the periproct in adults, it appears that there may be one fewer plate per column on the oral surface (Durham, 1949, text fig. 2, f), although the poor preservation of the margin of this specimen makes it possible that the smaller number of plates is only apparent. In all other species the number of plates on the oral surface is the same. Even *D. laevis* (fig. 21, d), which in some respects is the most widely divergent member of the genus, has the same number and general arrangement of the plates. It would appear from the study of this one genus that the arrangement and number of plates on the oral surface is a rather constant character, although this is not confirmed by a study of the species commonly assigned to the genus *Astro dapsis*.

The Genus *Astro dapsis*

Various species of the extinct genus *Astro dapsis* are highly diverse in their gross morphology and thus afford an excellent opportunity to investigate possible systematic changes in the arrangement of the plates of the oral surface. Unfortunately, since there rarely are large numbers of adequately preserved specimens of a species from a single locality, infraspecific variation cannot be well studied; but there appears to be no reason why it should be greater than in the genus *Dendraster*. Specimens representing the type species, *A. antiselli* Conrad (1866) (not Kew, 1920), *A. salinasensis* Richards (*A. antiselli* Kew, not Conrad, a species of simple morphology), *A. grandis* Kew, *A. whitneyi* Rémond, *A. gregersoni* Grant and Eaton (a gerontic species with highly raised petals), and *A. brewerianus* (Rémond) were studied (fig. 22).

In general, all the species mentioned above have the same arrangement and basic number of plates on the oral surface except close to the ambitus. In *A.*

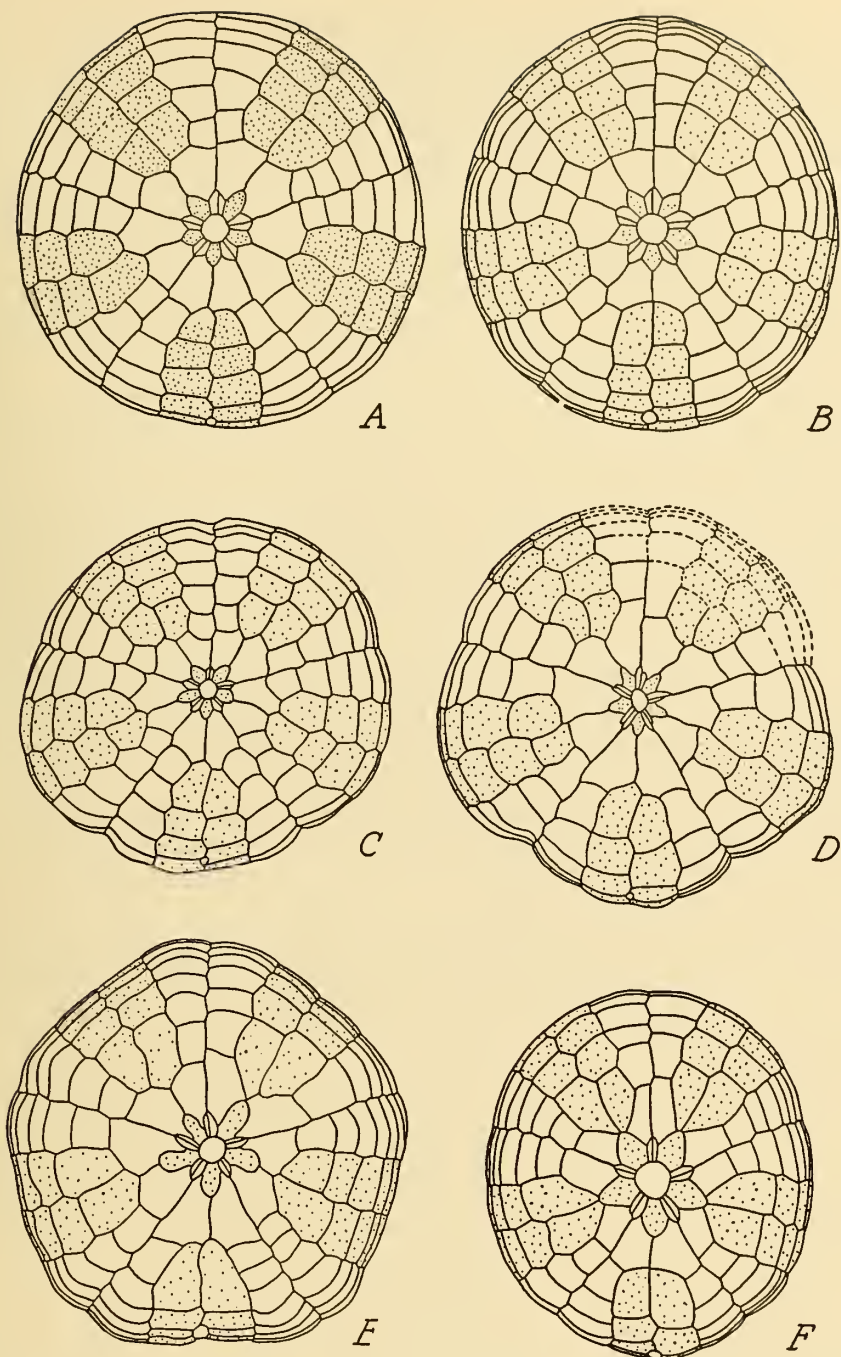


Fig. 22. Structure of oral surface of clypeasteroid echinoids: *a*, *Astrodapsis antiselli* Conrad, $\times 0.88$, oral view, hypotype no. 11030; Pliocene, California. *b*, *Astrodapsis salinasensis* Richards, $\times 1$, oral view, hypotype no. 11373; upper Miocene, California. (*A. antiselli* Kew not Conrad.) *c*, *Astrodapsis grandis* Kew, $\times 0.5$, oral view, "cotype" no. 11046; upper Miocene, California. *d*, *Astrodapsis whitneyi* Rémond, $\times 0.86$, oral view, hypotype no. 11036, in part restored; upper Miocene, California. *e*, *Astrodapsis gregersoni* Grant and Eaton, $\times 1$, oral view, paratype no. 34018, post-basical plates 2 and 3 fused together in ambulacrum IIa; upper Miocene, California. *f*, *Astrodapsis brewerianus* (Rémond), $\times 1.7$, oral view, hypotype no. 11016; upper Miocene, California.

brewerianus (fig. 22, f)—a species which is much smaller, less specialized, and geologically older than the others—there are not as many small plates next to the ambitus on the oral side. A specimen of *A. brewerianus* (length 28.3 mm.) has 16 post-basicoronal plates in interambulacrum 5b outside the genital plate; on the “cotype” (no. 11046) of *A. grandis* (length 94 mm., fig. 22, c) there are 19 plates in the same interval. Considering the disparity in size of the two species (the individuals are about average size for their respective species), there is relatively little difference in total number of plates. Furthermore, *A. brewerianus* is of about middle Miocene age and is presumably near to the ancestral stock, whereas *A. grandis* is of upper Miocene age and a rather highly specialized species. The few small plates on the oral side next to the ambitus of *A. brewerianus* are probably a primitive character. A survey of this feature in the various species studied shows that there is variation in the number of small plates next to the ambitus on the oral surface, and that this variation is independent of the size of the specimen (all adults), of the geologic age of the species, and usually of the degree of geronticism (or lack of it) as expressed by excessive development of some morphologic character. However, *A. gregersoni* (fig. 22, e), which is the most gerontic species studied in that it has excessively raised petals on the aboral surface, also has the greatest number of small plates on the oral surface next to the ambitus. There is much more variation in this feature in this genus than in *Dendraster*; however, this may be correlated with the greater specific variation in gross morphology in *Astrodapsis* than in *Dendraster*, in which most of the specific variation is in features other than gross morphology.

Variation in shape of individual plates is considerable in different individuals as well as in different species. In one specimen of *A. gregersoni* (fig. 22, e), in ambulacrum IVa, a single plate obviously occupies the position of two plates in other specimens of the same species.

In the species of *Astrodapsis* the periproct is situated either at the junction of the sutures between the fourth and fifth post-basicoronal plates (*A. antiselli*, fig. 22, a) or at the junction of the sutures between the third and fourth plates, or between the two positions.

In *A. brewerianus*, in accordance with its early age and nearness to the ancestral stock, the plates of interambulacra 1, 2, 3, and 4 are still in contact with the basicoronal plates of those areas, but in interambulacrum 5 the post-basicoronal plates are well separated. In all other species examined the post-basicoronal plates normally are well separated from the basicoronal plates. In the specimen of *A. gregersoni* previously noted as being anomalous in ambulacrum IV, the adjacent interambulacrum 3 has one plate in contact with the basicoronal plate.

In the species examined, the basicoronal plates are all fairly large, the interambulacral plates usually being somewhat larger than the ambulacral plates; but considerable variation exists among the different species. *A. antiselli* and *A. salinasensis* have more or less normally proportioned basicoronal plates, but *A. whitneyi* (fig. 22, d) and *A. gregersoni* have an accentuated geronticism expressed in their irregular basicoronal interambulacral plates. In most species there is a tendency for the basicoronal plate of interambulacrum 3 to be larger than the others.

TABLE 2
VARIATION IN NUMBER OF PLATES ON ORAL SURFACE IN ADULTS OF
Echinarachnius parma (Lamarck) FROM WOODS HOLE, MASS.

Oral Surface		
Column	No. of plates	No. of specimens
Interambulacrum Ia.....	3	85
	4	12
	1 adventitious	1
Interambulacrum Ib.....	2	3
	3	95
	1 adventitious	1
Interambulacrum 2a.....	2	1
	3	93
	4	4
Interambulacrum 2b.....	3	4
	4	94
Interambulacrum 3a.....	3	13
	4	85
Interambulacrum 3b.....	3	95
	4	3
Interambulacrum 4a.....	2	4
	3	93
	4	1
Interambulacrum 4b.....	2	1
	3	91
	4	6
Interambulacrum 5a.....	2	22
	3	76
Interambulacrum 5b.....	2	3
	3	95
	2 adventitious	2
Aboral Surface		
	No. of plates	No. of specimens
Interambulacrum Ia.....	8	1
	9	1
	10	19
	11	25
	12	10
	13	1
Ambulacrum Ia—inside petal.....	45-67 (median 55)	
Ambulacrum Ia—outside petal.....	6	3
	7	47
	8	6*

* In the 44 remaining specimens the number of plates is uncertain, but the usual number appears to be 7.

It would appear that in the genus *Astrodapsis* the number, general shape, and arrangement of the plates inside the area immediately adjacent to the ambitus are features that are characteristic of the genus, but that specific details within that framework are somewhat variable on both an intraspecific and an interspecific basis.

The Species *Echinarachnius parma*

Studies of the variation (tables 2 and 3) in plate arrangement (figs. 23 and 24) on the oral surface of *E. parma* indicate that this species is more variable than any other species studied for variation. From observations on the most closely

TABLE 3
RELATIONSHIP OF INTERAMBULACRAL AREAS TO BASICORONAL PLATES IN
Echinarachnius parma (Lamarck)

Woods Hole, Massachusetts; 100 specimens

Interambulacral area 1 in contact with basicoronal plates.....	62 specimens
Interambulacral area 2 in contact with basicoronal plates.....	79 specimens
Interambulacral area 3 in contact with basicoronal plates.....	85 specimens
Interambulacral area 4 in contact with basicoronal plates.....	73 specimens
Interambulacral area 5 in contact with basicoronal plates.....	30 specimens

Hampton Harbor, New Hampshire, 21 specimens

A much more variable (externally) suite of specimens than the Woods Hole collection

Interambulacral area 1 in contact with basicoronal plates.....	17 specimens
Interambulacral area 2 in contact with basicoronal plates.....	19 specimens
Interambulacral area 3 in contact with basicoronal plates.....	20 specimens
Interambulacral area 4 in contact with basicoronal plates.....	16 specimens
Interambulacral area 5 in contact with basicoronal plates.....	15 specimens

related genera and species, it is apparent that the restricted family to which it belongs is usually characterized by the separation of the post-basicoronal plates from the basicoronal plates in interambulacrum 5, and in most species by the separation in interambulacra 1 and 4 as well. From table 3 it can be seen that in two localities this separation of interambulacrum 5 varies markedly—70 per cent separation in one and 33 per cent in the other. The separation in the other areas likewise varies considerably. Even the number of plates on the oral surface (table 2) varies to a notable degree.

From a number of characters, such as the open petals, relatively simple food grooves, and slight elongation of the outer member of the pore-pairs, it is apparent that *E. parma* is an unspecialized species, presumably similar to the ancestral stock which gave rise to the restricted family. *Astrodapsis* is a specialized genus of the same family. Perhaps the variability in this species reflects the genetic potential in the ancestral stock which caused it to give rise to other genera as side branches of the main stock.

OTHER GENERA

Numerically significant and adequate material for variation studies of species in other genera was not available. Of the more than twenty-five specimens of *Helio-phora orbiculus* examined, only six can be considered adult. In five of the six, the

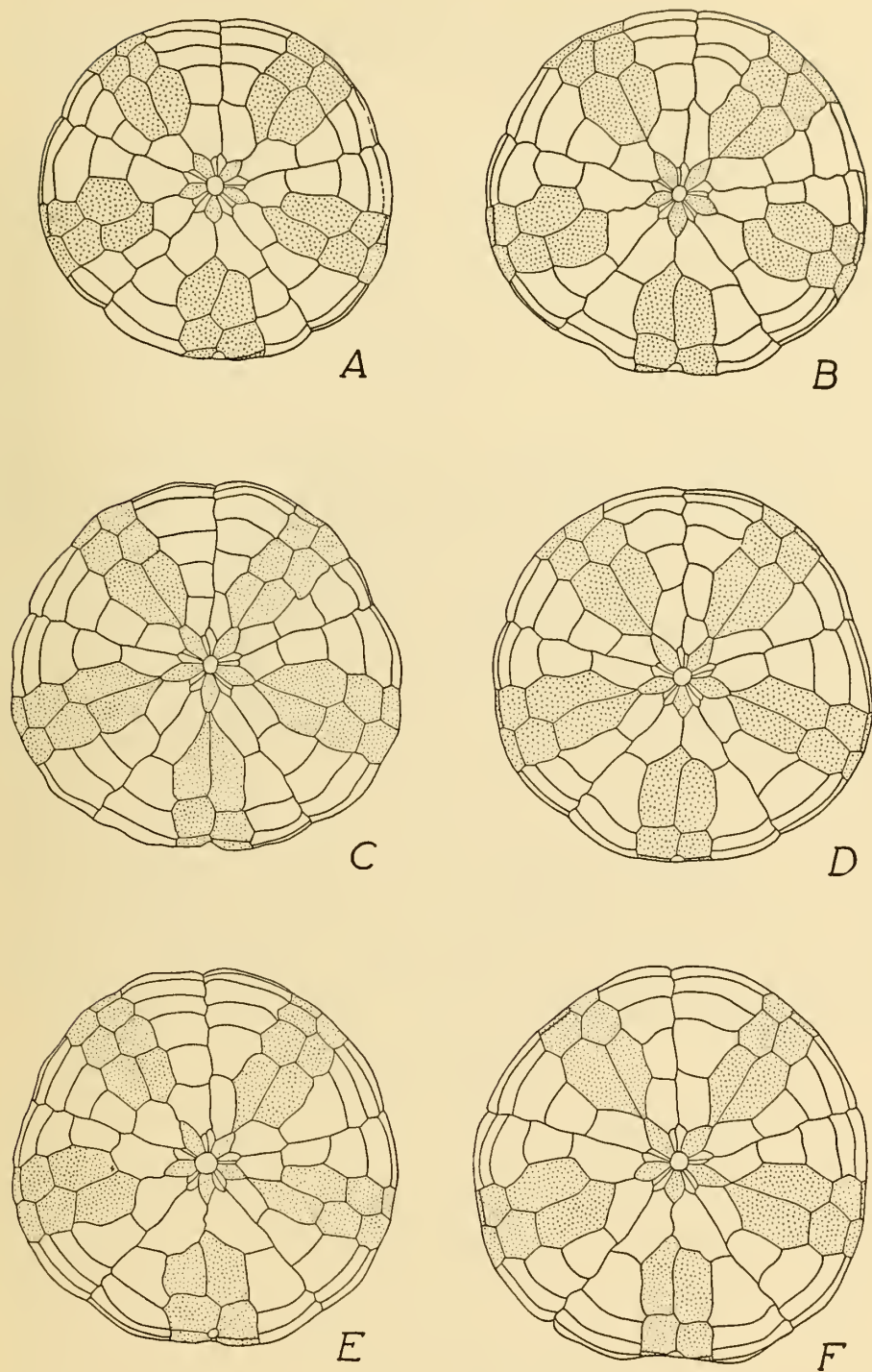


Fig. 23. Variation in structure of oral surface of *Echinarachnius parma* (Lamarek), $\times 0.9$; Recent, Woods Hole, Mass. Figs. a-f, respectively, after hypotypes nos. 35616, 35617, 35618, 35619, 35620, 35621.

four anterior interambulacral areas are separated from the basicoronal row. In the sixth (fig. 19, *g*), areas 1 and 3 are in contact. In the larger juveniles the areas are partly in contact, and in the smaller ones all in contact. All the specimens have five extra plates in the basicoronal row.

In the genus *Clypeaster*, examples and figures (Mortensen, 1948) of many species have been examined. The plates of the oral surface of six divergent types are illustrated (fig. 25, *a-f*). All the species examined (more than 20), ranging in age from the upper Eocene to the Recent, have the interambulacral areas separated and the basicoronal interambulacral plates smaller—usually much smaller—than the ambulacral plates. Usually the areas are separated by two pairs of ambulacral plates (fig. 25, *a-d, f*), but in the small *C. reticulatus* (fig. 25, *e*) only one pair separates the interambulacral areas. In *Clypeaster*, adventitious plates are rather common (fig. 25, *b* and *c*); some are obviously due to injury, but others are without any apparent cause.

In the genus *Cubanaster*, fifty or more specimens were available, but only half a dozen were suitable for examination without extended preparation. In the specimens examined, the arrangement of the plates is very constant. In the few specimens representing other species of the Neolaganidae a similar constancy seems to be apparent.

Examination of one or two specimens of many other genera and species widely distributed among the clypeasteroids seems to confirm the conclusion, based on the observations recorded above, that, except in a few presumably primitive and thus plastic stocks, the arrangement of the plates on the oral surface and of the adapical part of the interambulacra of adults is a character of major importance in the classification of the group. The relative size, arrangement, and character of the basicoronal ambulacral and interambulacral plates; whether or not the interambulacra are continuous on the oral surface; the number of plates between the periproct and the basicoronal row; the relative proportions and arrangement of the immediate post-basicoronal plates of the oral surface (but not necessarily the plates next to the ambitus); the presence of one or two columns of plates at the head of the interambulacra; the presence of simple or "compound" plates within the petals—these are significant structural features to be considered in the classification of clypeasteroid echinoids.

SYSTEMATICS

In the following classification, an attempt has been made to draw on all available data, both from the fossil record and from the living echinoids. Since many of the fossils have no living descendants, the data may at times be noncomparable between groups. In the classification, primary emphasis has been placed on the structural organization of the test. Superimposed on this are the relationships and differences indicated by the external morphology and structures, and the interior structures. In addition, the factors of geologic and geographic range either suggest or preclude certain associations or conclusions. Because the pedicellariae and spines are rarely found associated with the test in the fossil record, conclusions based on them are restricted to the higher categories with living representatives.

All specimen numbers unless otherwise stipulated, refer to the invertebrate

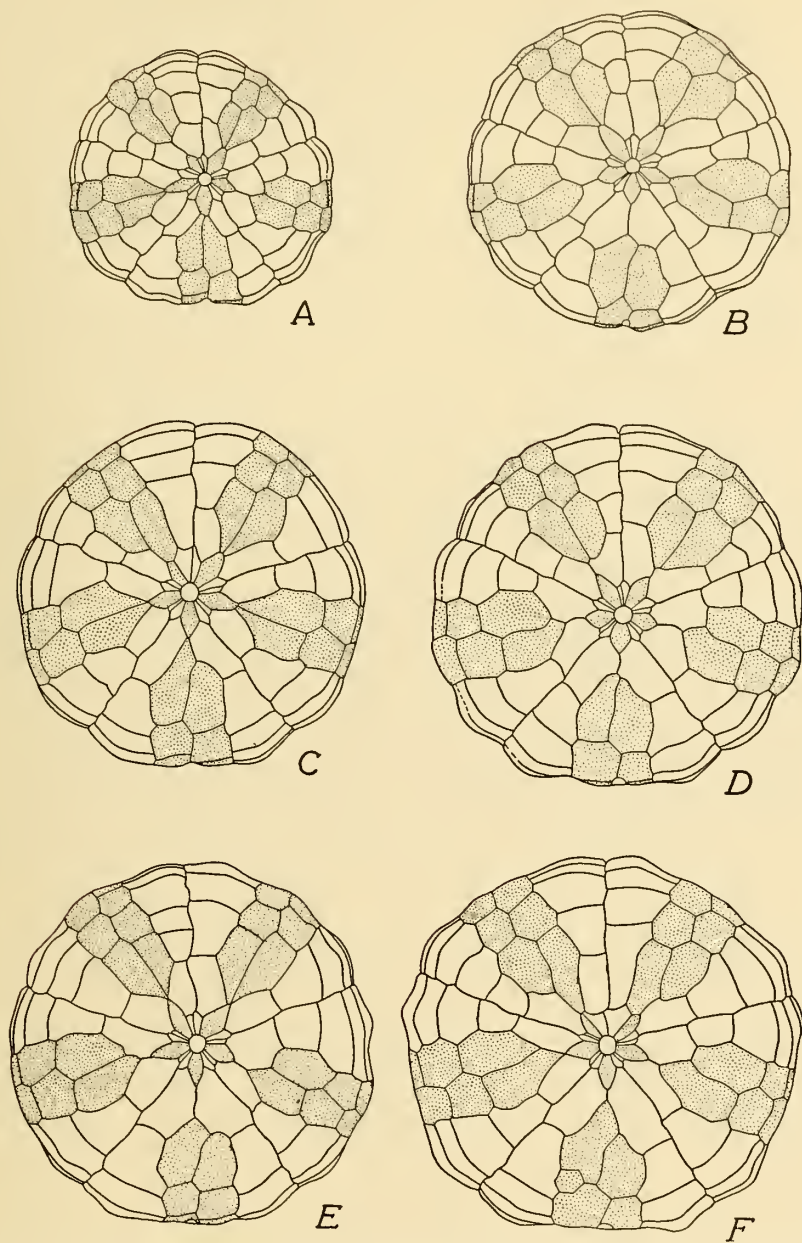


Fig. 24. Variation in structure of oral surface of *Echinarachnius parma* (Lamarck), $\times 0.8$; Recent, New Castle, New Hampshire. Figs. a-f, respectively, after hypotypes nos. 35622, 35623, 35624, 35625, 35626, 35627.

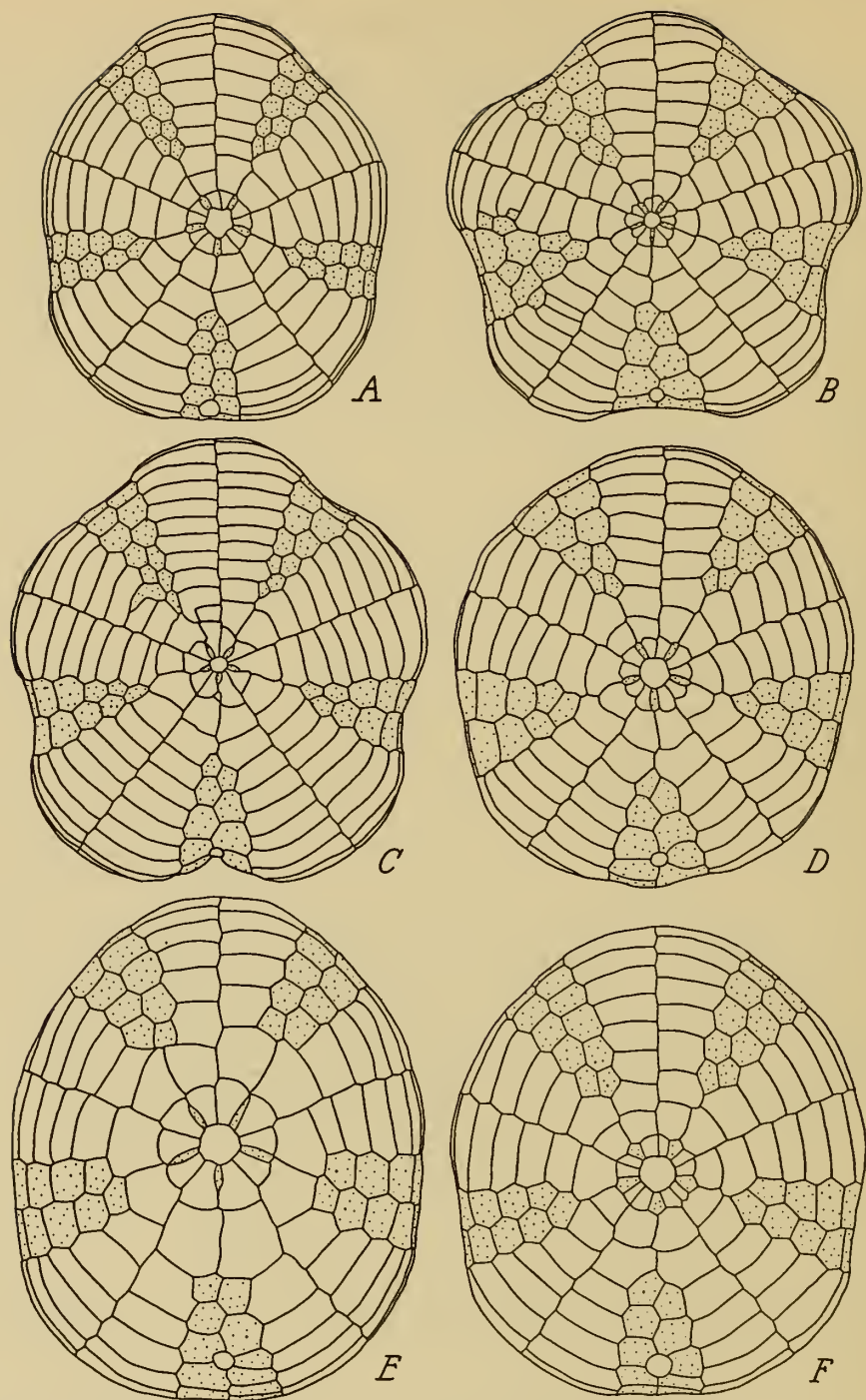


Fig. 25. Structure of oral surface of clypeasteroid echinoids: *a*, *Clypeaster rosaceus* (Linnaeus), $\times 0.44$, oral view, hypotype no. 33372; Recent, Florida. *b*, *Clypeaster ravenelii* (A. Agassiz), $\times 0.44$, oral view, hypotype no. 33381; Recent, Gulf of Mexico. *c*, *Clypeaster europacificus* H. L. Clark, $\times 0.32$, oral view, hypotype no. 33378; Recent, Gulf of Mexico. *d*, *Clypeaster prostratus* (Ravenel), $\times 0.84$, oral view, hypotype no. 33380; Recent, locality unknown. *e*, *Clypeaster reticulatus* (Linnaeus), $\times 1.54$, oral view, hypotype no. 33373; Recent, Philippine Islands. *f*, *Clypeaster speciosus* Verrill, $\times 0.69$, oral view, hypotype no. 33379; Recent, Gulf of California.

collections of the Museum of Paleontology of the University of California, Berkeley, California (abbreviated as U.C.M.P.).

Order CLYPEASTEROIDA L. Agassiz (1835), emended

Scutellidae Gray, 1825, *Ann. Philos.*, n.s., vol. 10, p. 427 (in part); d'Orbigny, 1853, *Paléont. Franc., Terr. Cret.*, vol. 6, p. 44 (in part).

Clypeastres L. Agassiz, 1835, *Mém. Soc. Sci. Nat. Neuchatel*, vol. 1, pp. 170, 182, 185 (in part).

Clypeastroides L. Agassiz, 1839, *Nouv. Mém. Soc. Helv. Sci. Nat.*, vol. 3 (Deser. des échinod. foss. de la Suisse), p. viii (in part); 1841, *Mon. d'Echin.*, Sec. Mon., Des Scutelles, p. 1; Desor 1842, *Mon. d'Echin.*, Trois. Mon., Des Galerites, pp. i, 1; L. Agassiz and Desor, 1847, *Ann. Sci. Nat.*, vol. 7, p. 129; Desor, 1858, *Synop. des échin. foss.*, p. 212; Dujardin and Hupé, 1862, *Hist. nat. des zooph. échinod.*, p. 554; Pomel, 1883, *Class. méth. et gén. échin. viv. et foss.*, p. 3.

Clypeastroidea L. Agassiz, 1840, *Cat. syst. ectyp. échin.*, pp. 3, 16 (in part).

Clypeasteridae d'Orbigny, 1851, *Cours elem. paléont. et de géol. strat.*, vol. 2, fasc. 1, p. 121; Wright, 1855, *Mon. Foss. Echinod. Oolitic Formations*, pp. 18, 21.

Clypeastroiden Quenstedt, 1852, *Handb. der Petrefactenk.*, p. 570 (in part).

Clypeastrida Haeckel, 1866, *Gen. Morph. der Organism.*, vol. 2, p. lxxv.

Clypeastrides Pomel, 1883, *Class. méth. et gén. échin. viv. et foss.*, pp. 67, 68.

Clypeastroida Duncan, 1889, *Jour. Linn. Soc. London, Zool.*, vol. 23, pp. 25, 142-144; Lambert and Thiéry, 1914, *Ess. nomencl. rais.*, p. 287; Mortensen, 1948, *Mon. Echin.*, vol. 4, pt. 2, p. 1.

Test inflated more or less ovoid to highly flattened; apical system compact, genitals fused; exocyclic, periproct oral to supramarginal, never close to apical system in adult; ambulacra petaloid adapically, usually wider than interambulacra on oral surface; ambulacral plates larger on oral surface than in petals; oral surface flattened except in unspecialized forms, no phylloides or bourrelets; internal supports more or less well developed except in a few unspecialized genera; peristome central, small, without gill slits; lantern well developed, without compass; auricles well developed, simple or fused; teeth keeled; primary tube feet respiratory, restricted to petals; numerous, often widely distributed, secondary tube feet; apical system usually central, fused; spines small, very numerous, usually differentiated into primaries and miliaries; tridentate, ophicephalous, triphyllous, and globiferous pedicellaria present.

Senonian to Recent, world-wide.

Remarks: On the basis of strict priority, the name *Scutelloidea* should be used for this order because it dates from Gray in 1825; but ever since L. Agassiz in 1835 (p. 182) used "Clypeastres" for one of his "trois familles naturelles" of the echinoids (the other two: "Spatangues" and "Cidarites"), the name *Clypeastres*, with varying terminations, has had almost universal usage. As first used by Agassiz it included all the irregular echinoids except the spatangoids; but in 1851 d'Orbigny used it in the modern sense, and since that time it has been almost universally used in the restricted sense.

Because the ambulacral areas are as wide as, or wider than, the interambulacral areas on the oral surface, recognition of this order is easy if the boundaries of the plates can be recognized. Often, however, the test requires special preparation before the sutures between the plates can be seen.

The wide oral ambulacral areas, the presence of a lantern with keeled teeth (fig. 10), and the occurrence of internal supports in all genera except a few with ovoid tests are the characters that give unity to the order. The presence of a single plate (fig. 12, *b-e*) at the head of the interambulacral areas in the laganinid and rotulinid echinoids is a specialized character modified from the pair (fig. 12, *a, f*) of plates at the head of these areas in the regular echinoids. Inasmuch as the

earliest known (Upper Cretaceous) clypeasteroid echinoids are referred to the laganinid genera *Fibularia* (*Echinoneus subglobosus* Goldfuss) and *Echinocyamus* (*Echinoneus placenta* Goldfuss, *Echinocyamus kamrupensis* Gupta), the question may be raised whether the order as defined is monophyletic or polyphyletic.

Since the genus *Scutellaster* Cragin has been shown to be a late Tertiary rather than a Cretaceous echinoid (Durham, 1953c), all recorded clypeasteroid echinoids other than the species noted above are of Cenozoic age. And since both clypeasterinid and scutellinid echinoids have two plates at the head of the interambulacra and this is a primitive rather than specialized condition like the single plate in the laganinid and rotulinid echinoids, it is apparent that several alternatives have to be considered to explain the situation. Three possible hypotheses are:

1. The various stocks (clypeasterinid, laganinid, scutellinid, and rotulinid) are derived from different ancestors and are convergent, presumably because of adaptation to a similar habitat, and thus should not be placed in a single order.

2. Paedogenesis or some similar process has occurred, and the clypeasterinid, scutellinid, and rotulinid stocks are derived from the laganinid stock.

3. The Mesozoic fossil record of the group is markedly incomplete, and clypeasterinid, scutellinid, and possibly rotulinid echinoids, as well as a common ancestor for the order, exist but have not yet been found.

Of the three hypotheses, the third is favored at present. The uniqueness of the wide ambulacra on the oral surface makes it seem improbable that convergent evolution has occurred, although the peculiar arrangement of the madreporite and some other features of the rotulinids might indicate a separate derivation for them. In the several ontogenetic sequences examined, no evidence of paedogenesis or similar retrogressive processes has been seen. Neither do the many individual species and genera of the Cenozoic support the second hypothesis. Within the groups, their geologic age and morphologic development all indicate an increasing degree of specialization throughout geologic time.

Hawkins (1912, 1920) and others have proposed that the clypeasteroid echinoids are derived from the Holoctypoida, though the Cretaceous genus *Discoidea* s.l. Hawkins (1920, p. 465) would derive the "Fibulariidae" and "Scutellidae" from *D. dixonii*, which is referable to the genus *Discoidea* proper, and the "Clypeastridae" from *D. cylindrica*, which is the type of the genus *Camerogalerus* Quenstedt. Thus, if Hawkins' derivations of the clypeasteroids are accepted, two separate orders would have to be recognized on phylogenetic grounds unless both of the discoidids and also their presumed ancestor (*D. subucula*) were also included in the order. Aside from this consideration, the derivation of the clypeasteroids as a whole from the discoidids is open to several objections, as follows:

1. All the discoidids possess internal radiating ridges on the oral surface, in positions similar to those of some of the more primitive clypeasteroids, yet one of the three oldest recorded clypeasteroids, *Echinoneus subglobosus* Goldfuss, if correctly referred to the genus *Fibularia*, presumably does not have radial partitions.

2. The Cretaceous laganinids, if correctly allocated generically, have single plates at the head of the interambulacra, whereas the discoidids have double plates.

3. The clypeasteroids all have the genital plates fused to the madreporite, whereas the discoidids have separate genital plates.

4. The discoidids have narrow ambulacra on the oral surface, whereas the clypeasteroids have the ambulacra as wide as, or wider than, the interambulacra.

5. The discoidids have a complex structure composed of several plates (Lovén, 1892, fig. p. 48) on the inside of the peristome for the attachment of the muscles supporting the lantern, whereas all clypeasteroids have either double or fused auricles, each apparently composed of a single "unit" for this purpose.

6. The periproct in the discoidids has migrated to a point where its mid-point is about half-way between the seventh and eighth pair of post-basicoronal plates; whereas (if Cotteau's 1889-1894 illustrations are correct) some of the early Tertiary clypeasteroids (e.g., *Scutellina hayesiana* L. Agassiz) appear to have more than eight post-basicoronal plates in the same position, which indicates that their ancestor had not reached the evolutionary stage of the discoidids in this respect.

None of the above objections by itself absolutely precludes the derivation of the clypeasteroids from the discoidids, but when the complex interplay of specialization, retrogression, and simplification that would be necessary to derive all the diverse clypeasteroid types from the already specialized discoidids is considered in the light of the points mentioned above, it seems highly unlikely that the discoidids can be considered the ancestral stock.

Although neoteny is a well-established process, paedogenesis seemingly is on much less secure ground; but unless paedogenesis or some similar process or processes are invoked in a highly complex and recurrent manner, the ancestral stock of the clypeasteroids, assuming that they are monophyletic, seemingly must have the following characters:

1. Ovoid to subspherical test with relatively unflattened oral surface.
2. No internal pillars or buttresses.
3. Five genital pores.
4. Periproct not closer to peristome than eighth post-basicoronal plate.
5. A lantern with keeled teeth in adult.
6. Simple, unfused auricles.
7. "Compound" ambulacral plates.
8. Primordial ambulacral and interambulacral plates retained in adult.
9. Small, relatively undifferentiated tubercles.
10. Interambulacra with two columns of plates adjacent to apical system.

As yet, such a possible ancestral form has not been recognized.

Within the order Clypeasteroida itself, it appears that the Cretaceous laganinids (*Echinoneus subglobosus* Goldfuss, *E. placenta* Goldfuss, and *Echinocyamus kamrupensis* Gupta) cannot be ancestral to most other clypeasteroids, because the periproct has already approached closer to the peristome than in most other genera. Likewise, the Cretaceous species presumably have fused auricles rather than primitive unfused auricles, and, if correctly allocated generically, they have only a single plate at the head of the interambulacral areas rather than a pair of plates as in the clypeasterinid and scutellinid genera. Similarly, it would appear that the Eocene-Oligocene neolaganinids with "compound" ambulacral plates cannot be descended from the above-noted species. Likewise, the scutellinid echinoids cannot be derived from the earliest recorded clypeasterinid species, for not only does the scutellinid genus *Eoscutella* appear earlier (middle Eocene) than the first *Clypeaster* (upper Eocene), but it has fused auricles rather than separate auricles. The rotulinid echinoids have several special characters that set them apart from the other clypeasteroids; but their seemingly late appearance (Miocene, or later,

Dartevelle, 1940) could allow their derivation from one of the other clypeasteroids. It would appear that if there is a common ancestor for the clypeasteroid echinoids, it must be pre-upper Senonian in age.

On the basis of the above considerations a suggested phylogeny (see frontispiece) has been prepared. *Discoidea*, or at least the later species of the genus, is not considered to be the ancestor of the order. The specialized nature of the late Upper Cretaceous fibulariids suggests that the four main branches of the clypeasteroid group must have been differentiated in either early Upper Cretaceous or late Lower Cretaceous time from an ancestor with unfused auricles and five genital pores. The advanced position of the periproct in the late Upper Cretaceous Fibulariidae indicates that this family and the neolaganid-laganid lineages had already diverged by that time. The "compound" plates in the petals of the Neolaganidae show that they are nearer the ancestral stock than the Laganidae.

The miliary spines of the Rotulina have a terminal crown like that of the Laganina and thus seemingly indicate a common derivation of the two suborders.

The separate auricles, together with the five genital pores and "compound" plates in the petals, seem to indicate that the Clypeasteridae are near the stem of the Clypeasteroida. Inasmuch as the Laganina have fused auricles it would appear that the clypeasterid radical must extend back into pre-late Upper Cretaceous time. From the fact that the basicoronal interambulacral plates are fairly large in the Arachnoididae (Ammotrophinae + Arachnoidinae) and reduced in the earliest Clypeasteridae, it would seem that these two lineages must have diverged in pre-upper Eocene time.

The earliest scutellinid known is the genus *Eoscutella*, which has only four genital pores but is specialized in its very large basicoronal interambulacral plates and bifurcating ambulacral food grooves. Seemingly it must be a side branch of the line leading toward the Echinarachniidae.

The next earliest member of the suborder Scutellina is the Protoscutellidae. They have five genital pores and thus are primitive in this respect; but the basicoronal ambulacral plates are already greatly reduced, a characteristic which indicates that they cannot be ancestral to any other family than the Mellitidae.

The Scutellidae are primitive in their nearly equal ambulacral and interambulacral basicoronal plates, but the bifurcating ambulacral food grooves and four genital pores are specialized. However, in general they seem to be as near the stem of the Scutellina as the Protoscutellidae. Presumably the echinarachniid lineage is derived from the scutellid ancestry, and it in turn from the ancestry of the protoscutellid-mellitid lineage. Since *Eoscutella* occurs in the middle Eocene and is already specialized, the scutellinid complex must have been derived from the clypeasterinid lineage in the Paleocene or Upper Cretaceous.

The Abertellidae seemingly could have been derived from the Scutellidae during the Oligocene by specialization. The geographic distribution of the Astrielypeidae would seem to associate them with the scutellid lineage, but the specialization of the basicoronal plates indicates an early divergence from the main stem.

The Echinarachniidae retain the primitive central stem in the ambulacral food grooves, and the basicoronal plates are not greatly specialized in most genera. They would seem to represent the stock from which the Dendrasteridae and Scutasteri-

dae have diverged by specialization. The presence of lunules in the three anterior ambulacra and their absence from the posterior ambulacra is a unique combination which has appeared only in the monogeneric family Scutasteridae.

The Monophorasteridae tend to extremely constricted interambulacra at the ambitus, and thus are unlike any of the other scutellinids. The characters of the basicoronal plates seem to indicate that they may have been derived from the echinarachniid ancestry early in the Cenozoic. The specialized interambulacra preclude any association with the Mellitidae, with which they have been placed by most investigators.

As an alternative to the more or less orthogenetic mode of evolution assumed in the above discussion, it might be suggested that the critical characters (fused auricles, simple ambulacral plates inside the petals, single column of plates at head of interambulacral areas, periproct close to peristome, four genital pores, internal supports, etc.) considered above are controlled either by unstable linked gene combinations or recessive genes in the clypeasteroid stock. If such is the case, the various sequences of associations of characters found might be caused by a series of crossovers of some of the linked genes, with consequent sorting and recombination of characters in which some of the original associations might reappear. However, these changes would have to be of a suprageneric rank, and it seems improbable that changes of this magnitude would have occurred within the clypeasteroids without occurring in other major echinoid groups.

Consideration of the characters of the head of the interambulacra, the auricles, the basicoronal plates, the madreporite, the miliary spines, the spicules in the sucking disc of the tube feet, the discontinuity of the interambulacra, and the arrangement of the plates within the petals, together with the known geologic record, indicates that the clypeasteroid echinoids should be divided into four major groups, which are here considered to be suborders.

Suborder CLYPEASTERINA L. Agassiz

Clypeastres, L. Agassiz, 1835, *Mém. Soc. Sci. Nat. Neuchatel*, vol. 1, pp. 170, 182, 185 (in part).
Clypeastrina, Gregory, 1900, *Lankester's Treat. on Zool.*, vol. 3, p. 316 (in part); Jackson, 1912, *Mem. Boston Soc. Nat. Hist.*, vol. 7, p. 204 (in part); Mortensen, 1948, *Mon. Echin.*, vol. 4, pt. 2, p. 5.

Test flattened or apically elevated, with internal supports; ambulacral plates "compound" (fig. 12, *a*) within petals, simple outside; interambulacra discontinuous on oral surface, terminated adapically by a pair of plates; apical system pentagonal or stellate, apices interambulacral; periproct inframarginal to supramarginal; auricles separate (fig. 9, *c, f, g*); aboral miliary spines simple (fig. 6, *a-c*), without crown or sack.

Upper Eocene to Recent, world-wide in tropical areas, warm temperate in Australia.

The "compound" plates within the petals are alternating primary and demi-plates (fig. 12, *a*) in contrast to the triads (fig. 27, *a, c*) which may occur in the Neolaganidae. The basicoronal interambulacral plate is separated (fig. 25) from the rest of the area by one and a half or more pairs of adjacent ambulacral plates, in contrast to the continuous interambulacra of the Laganina and Rotulina. All other clypeasteroids have fused auricles. The Clypeasterina, like the Laganina and Scutellina, have the apices of the madreporite interambulacral (fig. 1, *j*) in contrast to the Rotulina, in which the apices are ambulacral (fig. 1, *a* and *b*).

The simply terminating aboral miliary spines differentiate them from the Lagaina and Rotulina with terminal crowns and the Scutellina with terminal sacks.

The food grooves, number of genital pores, "combed" areas, character of basiconoral plates and buccal membrane, and other features indicate the presence of two well-defined families in this suborder.

Family Clypeasteridae L. Agassiz, emended

Clypeastres L. Agassiz, 1835, Mém. Soc. Sci. Nat. Neuchatel, vol. 1, pp. 170, 182, 185 (in part).
Clypeasteridae d'Orbigny, 1851, Cours. elem. paléont. et de géol. strat., vol. 2, fasc. 1, p. 121 (in part).

Clypeastridae Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 148; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 5.

Euclypeastridae Haeckel, A. Agassiz, 1872, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 375; *ibid.*, 1873, p. 620 (in part); Tenison-Woods, 1877, Proc. Linn. Soc. N.S.W., vol. 2, p. 168 (in part).

Echinanthidae A. Agassiz, 1872, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 376; *ibid.*, 1873, p. 620.

Test low to high; oral ambulacral food grooves simple, poorly defined; 5 genital pores; periproct marginal to submarginal; peristome usually in a well-defined infundibulum; buccal membrane naked; basiconoral interambulacral plates usually greatly reduced (fig. 15, *a* and *b*) never larger than ambulacral plates; no "combed" areas.

Upper Eocene (Auversian) to Recent, world-wide in tropical seas.

The five genital pores, lack of well-defined food grooves, and absence of linearly arranged, secondary tube-feet pores ("combed" areas) outside the petals readily differentiate this family from their closest relatives, the Arachnoididae.

At least 355 named fossil species (Mortensen, 1948, p. 19) and 30 living species have been referred to this family. The fossil record is especially notable in the circum-Tethyan and Caribbean-Gulf of Mexico areas. The morphologic diversity among these species is very great, and in consequence more than 30 supraspecific taxa have been named. Checchia-Rispoli (1920, 1925), Mortensen (1948), Roman (1952), and a few others have tried to create some order among these names and to reduce them in number, but the criteria used and the results obtained do not seem to be very utilitarian. The results of the present studies seem to indicate that all the diverse morphologies and variations grade into one another without any observable breaks. Certainly there are no structural changes in the test make-up comparable to those in the other families of clypeasteroid echinoids. It seems illogical that such diverse morphologies as are present in this family should not have structural differences comparable to those of the other families with much less diverse morphology, but the present studies have shown no indication of such differences. Accordingly, it seems best to recognize only the single genus *Clypeaster* and to reduce all the other taxa to synonyms. As a secondary conclusion of these studies, it seems highly probable that the number of named fossil species should be greatly reduced, many being merely variants of morphologically highly variable species.

Genus *Clypeaster* Lamarck

Echinanthus Leske, 1778, Add. ad Klein, p. 185 (in part); Meuschen, 1778, Mus. Gronov., p. 91 (in part); Gray, 1825, Ann. Philos., n.s., vol. 26, p. 427; d'Archiac and Haime, 1853, Deser. des anim. foss. du Numm. de l'Inde, p. 207; d'Orbigny, 1854, Rev. et Mag. Zool., ser. 2, vol. 6,

- pp. 18, 21-24; Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 3; A. Agassiz, 1872, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, pp. 106, 310; Tenison-Woods, 1878, Proc. Linn. Soc. N.S.W., vol. 2, p. 169.
- Clypeaster* Lamarek, 1801, Syst. anim. sans vert., p. 349; 1816, Hist. nat. anim. sans vert., vol. 3, p. 12; L. Agassiz, 1835, Mém. Soc. Sci. Nat. Neuchatel, vol. 1, p. 187; Des Moulins, 1835, Actes Soc. Linn. Bordeaux, vol. 7, p. 15; L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 129; Desor, 1858, Synop. des échin. foss., p. 239; A. Agassiz, 1872, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 306; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 68; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 298; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 37-39. Not Dejean, 1821.
- Scutum* Schumacher, 1817, Ess. hab. vers. test., pp. 33, 85.
- Nyctimene* Gistel, 1848, Naturgesch. des Thierreichs für h. Schülern, p. 175, not *Nyctimene* Borkhausen, 1797, nor Morris, 1837.
- Rhaphidoclypus* A. Agassiz, 1863, Bull. Mus. Comp. Zoöl. Harvard Coll., vol. 1, p. 25.
- Stolonoclypus* A. Agassiz, 1863, Bull. Mus. Comp. Zoöl. Harvard Coll., vol. 1, p. 25.
- Alexandria* Pfeffer, 1881, Verh. naturw. Ver. Hamburg, ser. 2, vol. 5, p. 63.
- Echinorodorum* Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 68.
- Pavaya* Pomel, 1883, Class. méthod. et gén. des échin. viv. et foss., p. 68.
- Anomalanthus* Bell, 1884, Proc. Zool. Soc. London, p. 43.
- Bunactis* Pomel, 1887, Paléont. Algerie, vol. 2, fasc. 2, p. 204.
- Laganidea* Pomel, 1887, Paléont. Algerie, vol. 2, fasc. 2, p. 172.
- Miophyma* Pomel, 1887, Paléont. Algerie, vol. 2, fasc. 2, p. 260.
- Oxypleura* Pomel, 1887, Paléont. Algerie, vol. 2, fasc. 2, p. 221, not Amyot and Serville, 1843.
- Paratina* Pomel, 1887, Paléont. Algerie, vol. 2, fasc. 2, p. 190, not Mik, 1874.
- Platypleura* Pomel, 1887, Paléont. Algerie, vol. 2, fasc. 2, p. 174, not Amyot and Serville, 1843.
- Pliophyma* Pomel, 1887, Paléont. Algerie, vol. 2, fasc. 2, p. 247.
- Diplotheicanthus* Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 153.
- Plesianthus* Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 154.
- Biarritzella* Boussac, 1911, Ann. Hébert, vol. 5, p. 30.
- Dactylanthus* Lambert, 1912, Mém. Soc. Paléont. Suisse, vol. 38, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 2, p. 89, not Carlgren, 1911.
- Eurycoila* Lambert, 1912, Mém. Soc. Paléont. Suisse, vol. 38, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 2, p. 90.
- Eurypleura* Lambert, 1912, Mém. Soc. Paléont. Suisse, vol. 38, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 2, p. 90, not Kaup, 1858.
- Paleanthus* Lambert, 1912, Mém. Soc. Paléont. Suisse, vol. 38, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 2, p. 89.
- Coronanthus* Lambert, 1913, Mém. Soc. Paléont. Suisse, vol. 39, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 3, p. 123.
- Oxyclypeina* Lambert and Thiéry, 1913, in Lambert, Mém. Soc. Paléont. Suisse, vol. 39, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 3, p. 122, pro *Oxypleura* Pomel, 1887, not Amyot and Serville, 1843.
- Paratinanthus* Lambert and Thiéry, 1913, in Lambert, Mém. Soc. Paléont. Suisse, vol. 39, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 3, p. 122, pro *Paratina* Pomel, 1887, not Mik, 1874.
- Platyclypeina* Lambert and Thiéry, 1913, in Lambert, Mém. Soc. Paléont. Suisse, vol. 39, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 3, p. 122, pro *Platypleura* Pomel, 1887, not Amyot and Serville, 1843.
- Tholeopelta* Lambert and Thiéry, 1913, in Lambert, Mém. Soc. Paléont. Suisse, vol. 39, Deser. échin. des terr. Néogènes du bass. du Rhone, fasc. 3, p. 122, pro *Eurypleura* Lambert, 1912, not Kaup, 1858.
- Alexandraspis* Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 315, pro *Alexandria* Pfeffer, 1881, not *Alexandrium* Molin, 1860.
- Guebhardanthus* Lambert, 1914, Ann. Soc. Linn. Lyon, vol. 61, p. 17.
- Laubeanthus* Lambert, 1914, Ann. Soc. Linn. Lyon, vol. 61, p. 19.

Leptoclypus Koehler, 1922, Echinod. Indian Mus., pt. 9, pp. 31-32.

Orthanthus Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 34.

Zanolettia Sanchez Roig, 1951, Mem. Soc. Cubana Hist. Nat., "Felipe Poey," vol. 20, p. 39.

Herrerasia Sanchez Roig, 1952, Rev. Agric. Habana, Julio, 1952, p. 137.

Rojasaster Sanchez Roig, 1952, Rev. Agric. Habana, Julio, 1952, pp. 135-136.

Type species: Clypeaster Lamarck—*C. rosaceus* Lamarck = *Echinus rosaceus* Linnaeus, subs. desig. Des Moulins, 1835; *Echinanthus* Gray—*E. rosaceus* (Linnaeus) = *Echinus rosaceus* Linnaeus, subs. desig. Gray, 1851; *Scutum* Schumacher—*S. rosaceum* Schumacher = *Echinus rosaceus* Linnaeus, monotypic; *Nyctimene* Gistel—*N. rosaceus* Gistel = *Echinus rosaceus* Linnaeus, here designated; *Rhaphidoclypus* A. Agassiz—*Clypeaster reticulatus* (Linnaeus) (in part) = *Rhaphidoclypus scutiformis* A. Agassiz, subs. desig. Lambert and Thiéry, 1914; *Stolonoclypus* A. Agassiz—*Clypeaster humilis* (Leske), emended = *Stolonoclypus placunarius* A. Agassiz = *Scutella placunaria* Lamarck, subs. desig. Lambert and Thiéry, 1914; *Alexandria* Pfeffer—*A. magnifica* Pfeffer = (?) *C. europacificus* Clark, monotypic; *Echinorodorum* Pomel—*E. rosaceus* (Linnaeus) = *Echinus rosaceus* Linnaeus, here designated; *Pavaya* Pomel—*P. corwini* (Pavay) = *Clypeaster corwini* Pavay, monotypic; *Anomalanthus* Bell—*Echinanthus tumidus* Woods, monotypic; *Bunactis* Pomel—*C. scillae* Des Moulins, subs. desig. Lambert, 1912; *Laganidea* Pomel—*C. scutellaeformis* Pomel, subs. desig. Lambert, 1912; *Miophyma* Pomel—*C. altus* Lamarck, here designated; *Oxypleura* Pomel—*C. dorma* Pomel, subs. desig. Lambert, 1912; *Paratina* Pomel—*C. confusus* Pomel, subs. desig. Lambert and Thiéry, 1914; *Platypleura* Pomel—*C. marginatus* Lamarck, subs. desig. Lambert, 1912; *Pliophyma* Pomel—*C. atlas* Pomel, subs. desig. Lambert, 1912; *Diplotheanthus* Duncan—*Clypeaster reticulatus* Linnaeus of Lovén = *Echinus rosaceus* Linnaeus, not *C. reticulatus* Linnaeus, orig. desig.; *Plesianthus* Duncan—*Echinanthus testudinarius* Gray, orig. desig.; *Biarritzella* Boussac—*B. marbellensis* Boussac, orig. desig.; *Dactylanthus* Lambert—*C. acclivis* Pomel, orig. desig.; *Eurycoila* Lambert—*C. intermedius* Des Moulins, orig. desig.; *Eurypleura* Lambert—*C. duchassaingi* Michelin, orig. desig.; *Paleanthus* Lambert—*C. breunigi* Laube (Lambert, 1914, p. 14, says *C. breunigi* Fabiani not Laube), orig. desig.; *Coronanthus* Lambert—*C. microstoma* Lambert, monotypic; *Alexandraspis* Lambert and Thiéry—*Alexandria magnifica* Pfeffer, monotypic; *Guebhardanthus* Lambert—*C. priscus* Oppenheim, orig. desig.; *Laubeanthus* Lambert—*C. breunigi* Laube, orig. desig.; *Tholeopelta* Lambert and Thiéry—*C. duchassaingi* Michelin; *Leptoclypus* Koehler—*C. annandalei* Koehler, orig. desig.; *Orthanthus* Mortensen—*C. euclastus* Clark, orig. desig.; *Zanolettia* Sanchez Roig—*Z. zanolettii* Sanchez Roig, orig. desig.; *Herrerasia* Sanchez Roig—*C. profundus* Sanchez Roig, not *C. profundus* L. Agassiz, 1840, orig. desig.; *Rojasaster* Sanchez Roig—*R. hernandezi* (Sanchez Roig) = *C. hernandezi* Sanchez Roig, orig. desig.

(Figs. 1, *g*, *j*; 15, *a* and *b*; 25; 26, *a*, *n*; 28, *d*)

Medium-sized to large; test highly variable, flattened to highly elevated apically; oral surface flat to concave, usually with well-developed oral infundibulum; margin of test rounded to flattened and inflated; apical system and peristome central; petals variable, closed and rounded to wide open and sublyrate; outer pore of petals elongate, inner rounded, often connected by a well-defined furrow; periproct usually inframarginal, rarely marginal, situated at junction between third and fourth or fourth and fifth post-basicoronal interambulacral plates; buccal membrane naked, with imbedded irregular spicules; internal supports variable in abundance, consisting of thin laminae and pillars, most strongly developed in flattened species; wall of test sometimes double; primordial (basicoronal) interambulacral plates usually much smaller than ambulacral plates, separated from post-basicoronal plates by 1 to 3 pairs of ambulacral plates; 6 to 10 ambulacral and 4 to 6 interambulacral post-basicoronal plates on oral surface.

Upper Eocene (Auversian) to Recent, world-wide in tropical seas.

This genus is represented in all the tropical areas of the modern seas. During the Miocene it was abundant in the Mediterranean area, but it has no living species there. Presumably this may be due to the low temperatures that occur there in winter. Numerous species have also been described from the Caribbean-Gulf of Mexico area (Sanchez Roig, 1952, records fifty-seven species from Cuba, of which

fifty-three are of Oligocene and Miocene ages). The oldest American species known, *Clypeaster stefanini* Cottreau (fig. 28, *d*) is from beds of lower Oligocene age, but Lambert (1914) records Auversian species from Europe.

Mortensen (1948, p. 17) considers the genus to be largely littoral-sublittoral in habitat. Some species, however, have been recorded from a depth of 500 meters.

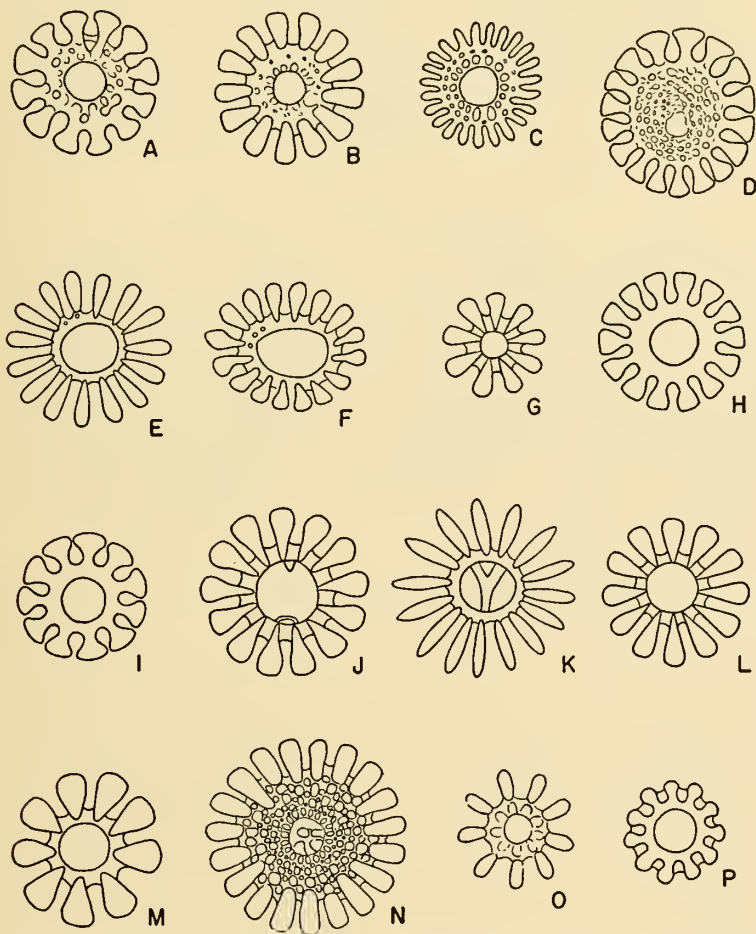


Fig. 26. Cross sections of primary spines of clypeasteroid echinoids: *a*, *Clypeaster reticulatus* (Linnaeus), $\times 150$. *b*, *C. humilis* (Leske), $\times 105$. *c*, *C. annandalei* Koehler, $\times 90$. *d*, *C. lamprus* H. L. Clark, $\times 80$. *e*, *Arachnoides placenta* (Linnaeus), $\times 135$. *f*, *Fellaster zelandiae* (Gray), $\times 135$. *g*, *Mortonia australis* (Des Moulins), $\times 180$. *h*, *Jacksonaster depressum* (Lesson), $\times 180$. *i*, *Hupea decagonalis* (Lesson), $\times 180$. *j*, *Dendraster excentricus* (Eschscholtz), $\times 150$. *k*, *Scaphechinus mirabilis* A. Agassiz, $\times 150$. *l*, *Echinarachnius parma* (Lamarek), $\times 150$. *m*, *Heliophora orbiculus* (Linnaeus), $\times 275$. *n*, *Clypeaster rosaceus* (Linnaeus), $\times 65$. *o*, *C. humilis* (Leske), $\times 140$, aboral. *p*, *Peronella japonica* Mortensen, $\times 150$. After Mortensen, 1948, figs. 15, *b*; 15, *a*; 42; 72, *a*; 88, *a*; 88, *b*; 104, *c*; 162, *c*; 162, *a*; 210, *c*; 210, *b*; 210, *a*; 258; 34; 52, *c*; and 187, *a*.

In this study, the oldest (lower Oligocene) American species, *C. stefanini* Cottreau (fig. 28, *d*), as well as the Recent *C. rosaceus* (Linnaeus), *C. ravenellii* (A. Agassiz), *C. europacificus* H. L. Clark, *C. prostratus* (Ravenel), *C. reticulatus* (Linnaeus), and *C. speciosus* Verrill, representing several of the named supra-

specific taxa, have been studied in detail (fig. 25, *a-f*). According to Mortensen's (1948) usage, the Recent species respectively fall within *Clypeaster s.s.*, *Orthanthus*, *Alexandria*, *Stolonoclypus*, *Rhaphidoclypus* and *Stolonoclypus*. *C. stefanini* is assigned to *Laganidea* by Lambert and Thiéry (1914). In addition to the preceding, figures showing the plates of the oral surface of numerous species and specimens of other species, such as *C. aegyptiacus*, have been examined. The differences in structure on the oral surface are slight, except for variation in total number of plates, and do not seem to be at all comparable in magnitude to the differences in much more closely similar (externally) species of laganinid and scutellinid echinoids. On a comparable basis with the other suborders, there does not seem to be any reason to separate different taxa within the Clypeasteridae.

Family Arachnoididae Duncan

Arachninae Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 158, 165.

Arachnoidinae Gregory, 1900, Lankester's Treat. on Zool., vol. 3, p. 318 (in part).

Echinarachnidae Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 314 (in part).

Arachnoididae Gregory, H. L. Clark, 1914, Mem. Mus. Comp. Zool. Harvard Coll., vol. 46, p. 43; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 132.

Test flattened, ambital margin moderately thin; ambulacral food grooves (fig. 2, *a*) simple, well defined, extending from peristome to apical system in later species, no secondary tube feet in grooves; secondary tube feet outside petals in dense oblique series (combs in advanced species), restricted to ambulacral areas (fig. 2, *e* and *f*); 4 genital pores; peristome not sunken; buccal membrane plated; basicoronal interambulacral plates externally larger (fig. 15, *c*) than ambulacral plates.

Miocene to Recent, Indo-Pacific.

The striking ambulacral "combed" areas (fig. 2, *e* and *f*), both within and without the petals, make this a very easily recognizable family, for the most part. In *Arachnoides placenta*, the combs cover essentially all of the ambulacral area on the apical surface and all except the basicoronal plates and a narrow zone along the interambulacral suture on the oral surface. On the available specimens of the Miocene *Monostychia australis*, the "combed" areas are not as well defined as in *A. placenta*; only occasionally are the secondary tube feet pores and the tubercles as perfectly aligned as they are in the younger species. In the Miocene species, the most distinct areas of recognized alignment are on the oral surface just inside the ambitus. No clear alignment was observed within the petals. The large basicoronal interambulacral plates, the plated buccal membrane, and lack of a peristomal infundibulum seem to make it unlikely that the arachnoidids are directly derived from the clypeasterids. However, the "compound" plates in the petals suggest that the two families have a common ancestor. It seems probable that arachnoidids older than *Monostychia*, *Fossulaster*, and *Scutellinoides* will be found.

The spines are very numerous and short. The primary spines of the combed areas are club-shaped, but those in other areas are not.

The character of the petals and types of internal supports delimit two well-marked subfamilies.

Subfamily Arachnoidinae Duncan

Arachninae Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 158, 165 (in part).

Arachnoidinae Gregory, 1900, Lankester's Treat. on Zool., vol. 3, p. 318 (in part).

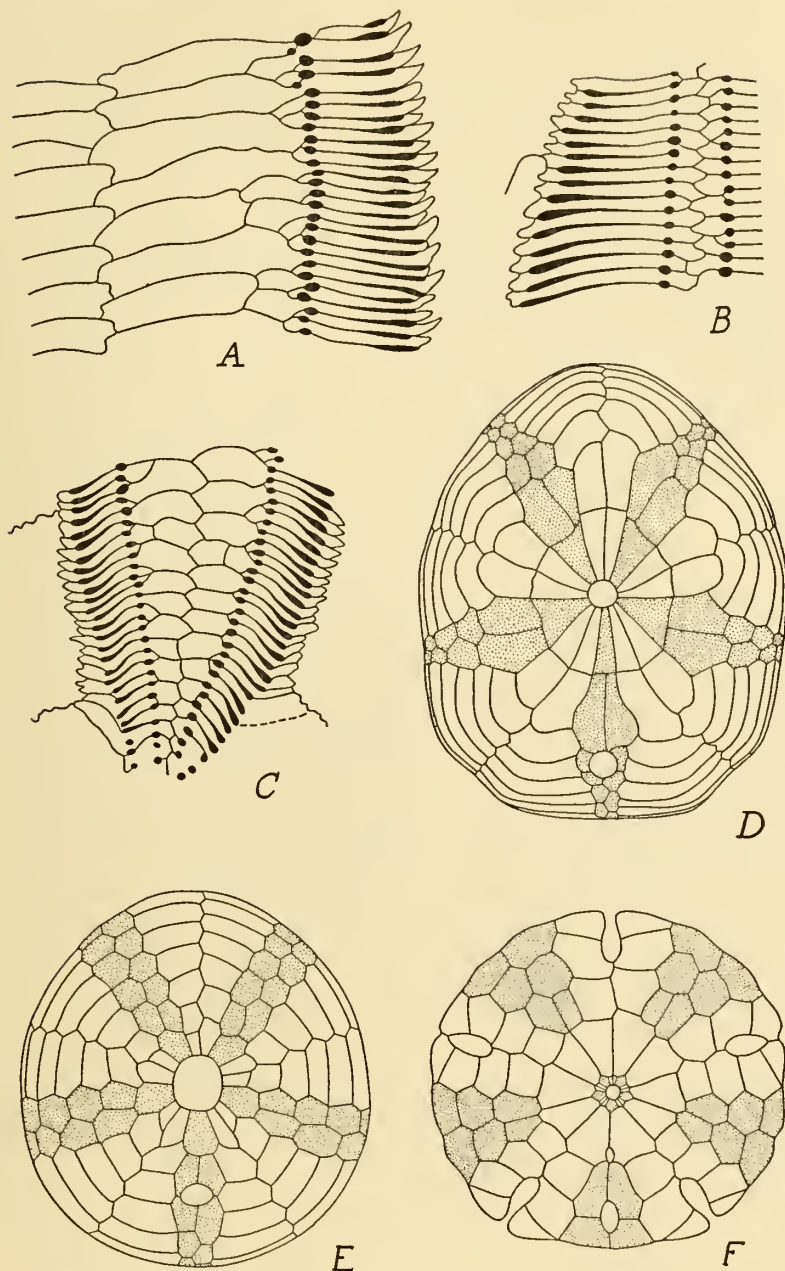


Fig. 27. Structure of neolaganid petals and of oral surface of clypeasteroid echinoids: *a*, *Neorumphia elegans* (Sanchez Roig), $\times 5.7$, medial part of right posterior petal, hypotype Sanchez Roig Collection; upper Oligocene, Cuba. *b*, *Sanchezella sanchezi* (Lambert), $\times 8.5$, medial part of right posterior petal, hypotype no. 33260; upper Eocene, Cuba. *c*, *Weisbordella caribbeana* (Weisbord), $\times 7.1$, outer part of left anterior petal, hypotype Sanchez Roig Collection; upper Eocene, Cuba. *d*, *Wythella eldridgei* (Twitchell), $\times 1.3$, oral view, hypotype no. 33261; upper Eocene, Cuba. *e*, *Sismondia murravica* Tate, $\times 3.7$, oral view, hypotype no. 34050; Miocene, Australia. *f*, *Mellitella stokesii* (L. Agassiz), $\times 1$, oral view, hypotype no. 33807; Recent, Ecuador.

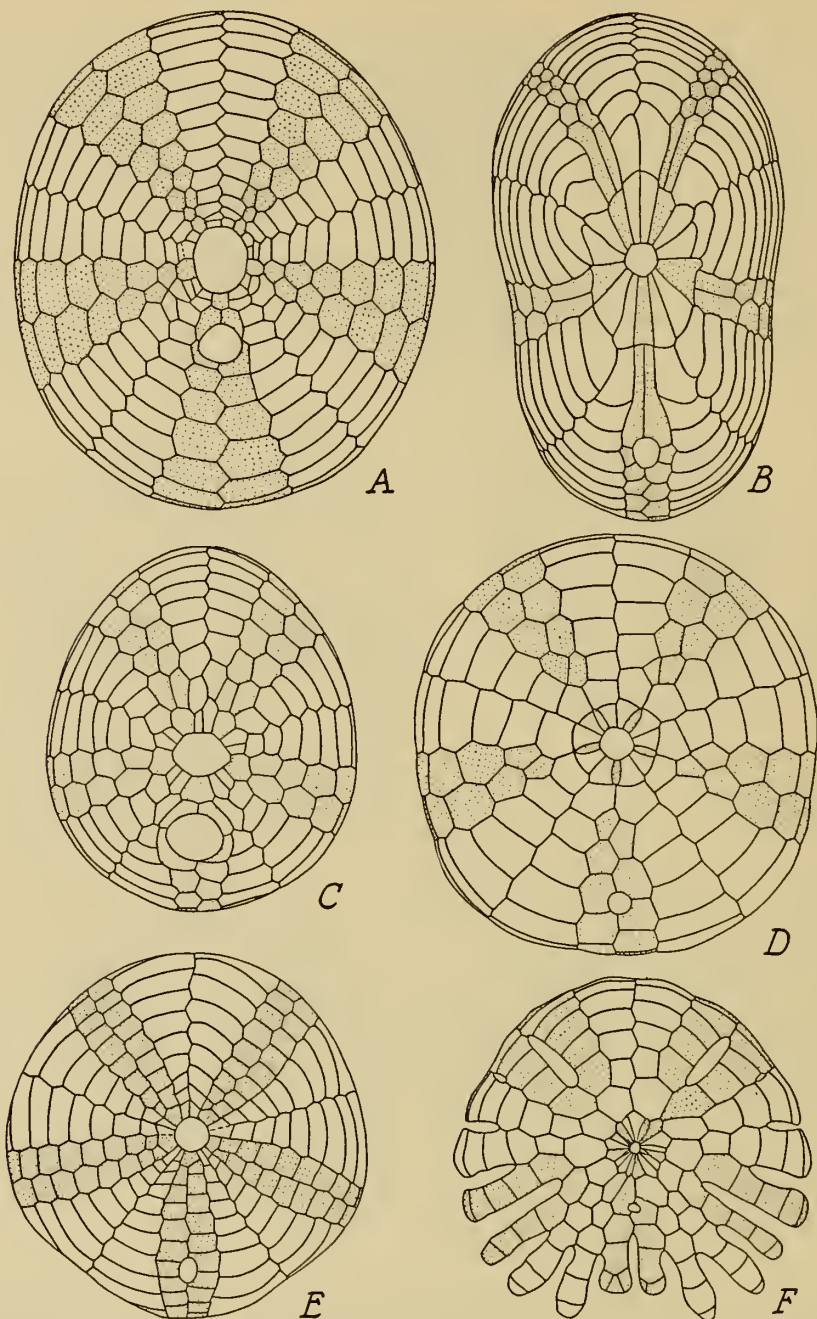


Fig. 28. Structure of oral surface of clypeasteroid echinoids: *a*, *Tarphhygus clarki* (Lambert), $\times 4.17$, oral view, hypotype Paleont. Res. Inst. no. 20512; upper Eocene, Cuba. *b*, *Sanchezella sanchezi* (Lambert), $\times 1.7$, oral view, after hypotype no. 33298; upper Eocene, Cuba. *c*, *Mortonia australis* (Des Moulins), $\times 3.4$, oral view, hypotype no. 33791; Recent, Hawaii. *d*, *Clypeaster stefanini* Cottreau, $\times 1.2$, oral view, hypotype no. 33360; lower Oligocene, Tampico, Mexico. *e*, *Proescutella caillaudi* Cottreau, $\times 8.8$, oral view, after Cottreau (1891, pl. 266, fig. 12); Eocene, France. *f*, *Rotula deciesdigitata* (Leske), $\times 0.71$, oral view, hypotype 33851; Recent, Loanda, Angola.

Echinarachnidae Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 314 (in part).

Arachnoididae Gregory, H. L. Clark, 1914, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 46, p. 43; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 132 (in part).

Periproct supramarginal; petals raised above interambulaera; internal supports in outer marginal zone only; combed areas large; ambulacral food grooves extending to apical system. Pliocene to Recent, Indo-Pacific.

Genus *Arachnoides* Leske²

Arachnoides Leske, 1778, Add. ad Klein, p. 26; Schumacher, 1817, Ess. hab. vers test., pp. 33, 85; L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, p. 94; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 165 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 142-144.

Echinarachnius Leske, 1778, Add. ad Klein, p. 217;³ Lambert and Thiéry, 1914, Ess. nomencl. rais., pp. 315-316.

Type species: *Echinus placenta* Linnaeus, monotypic.

(Figs. 2, *a, e, f*; 5, *g* and *h*; 6, *c*; 9, *g*; 15, *c*; 26, *c*; 29, *a*)

Petals wide open, raised; combed areas extending over all the ambulacral areas except for a narrow border along the suture between adjacent areas on the oral surface; food grooves extending from peristome to apical system, a similar but narrower groove from periproct to edge of basicoronal plates; periproct just slightly supramarginal; edge of test notched at periproct; only one pair of interambulacral plates (fig. 29, *a*) extending onto oral surface, so that there are two pairs of ambulacral plates meeting in interambulacrum 5, two and a half pairs in interambulaera 1 and 4, and three pairs in the anterior interambulaera; periproct between second and third pair of post-basicoronal interambulacral plates, with only the first pair on the oral surface; interambulacral plates not much wider than ambulacrals in basicoronal row; no large tubercles in interambulacral areas adjacent to apical system; pedicellaria usually bivalved; about twenty aboral plates in each interambulacral column.

Pliocene to Recent, Indo-Pacific.

The genus as restricted occurs from the Andaman Islands to Amoy, Samoa, Queensland, and Western Australia, but it seems to be absent from New Zealand. Prior records of its occurrence in New Zealand seem to be based on *A. zelandiae* Gray, which is here referred to *Fellaster* n. gen. It is known from the middle Pliocene of the East Indies and the lower Pliocene of Australia (H. L. Clark, 1946, p. 340). H. L. Clark (1938, p. 415) has reported that *A. placenta* is very abundant in fine, somewhat muddy sand in the intertidal area at Port Darwin. Mortensen (1948, p. 147) reports a few occurrences in depths of 57 meters, but most records are of intertidal occurrences.

Arachnoides tenuis H. L. Clark seems to be congeneric with *A. placenta*, but *A. zelandiae* Gray differs from *A. placenta* in characters which appear to be of greater than specific rank. In consequence, it is made the type species of the following new genus.

Genus *Fellaster* n. gen.

Type species: *Arachnoides zelandiae* Gray.

(Figs. 1, *f*; 8, *i*; 26, *f*; 29, *b*)

Petals wide open, raised; combed areas include about two-thirds width of ambulacral plates outside petals; food grooves extending from peristome to apical system, no groove from

² Placed on Official List of Generic Names by action of International Congress of Zoology, Paris, 1948. See Bull. Zool. Nomencl., vol. 4, p. 534, 1950.

³ Suppressed if necessary by action of International Congress of Zoology, Paris, 1948. See *ibid.*

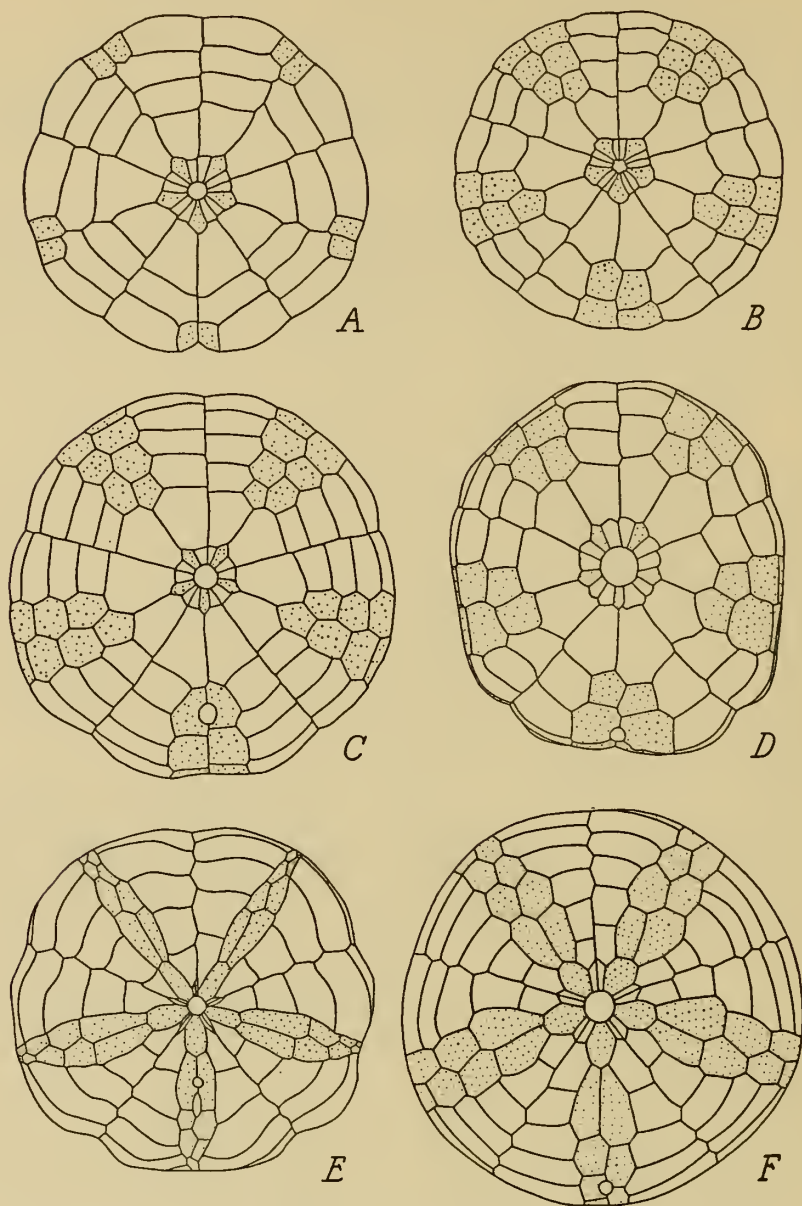


Fig. 29. Structure of oral surface of clypeasteroid echinoids: *a*, *Arachnoides placenta* (Linnaeus), $\times 0.8$, oral view, hypotype no. 33351; Recent, east coast of Sumatra. *b*, *Fellaster zelandiae* (Gray), $\times 0.6$, oral view, hypotype no. 33789; Recent, New Zealand. *c*, *Ammotrophus cyclius* H. L. Clark, $\times 0.8$, oral view, apparent plate arrangement as seen in Clark's (1928, fig. 140, *b*) and Mortensen's (1948, pl. 44, fig. 4) figures; details of basicoronal row uncertain; Recent, Australia. *d*, *Monostychia australis* Laube, about $\times 1.0$, oral view, hypotype no. 33848; Miocene, Australia. *e*, *Monophoraster darwini* (Desor), $\times 0.6$, oral view, hypotype no. 33358, Miocene, Patagonia. *f*, *Iheringiella patagonensis* (Desor), $\times 1.4$, oral view, specimen no. 76032, Dept. of Geology, Princeton University; Miocene, Patagonia.

periproct to margin of basicoronal plates; periproct distinctly supramarginal, situated at junction between third and fourth pairs of post-basicoronal interambulacral plates; edge of test not notched for periproct; on oral surface two post-basicoronal plates in interambulacral columns 1b, 4a, 5a, 5b, and three plates in columns 1a, 2a, 2b, 3a, 3b, and 4b; only one pair of ambulacral plates meeting across interambulacral suture on oral surface; basicoronal interambulacral plates much larger than adjacent ambulacral plates; few large tubercles in interambulacral areas adjacent to apical system; pedicellaria usually three-valved.

Pliocene to Recent, New Zealand.

Fellaster may be differentiated from *Arachnoides* by the lack of the periproctal groove and marginal notch; by the larger number of interambulacral plates on the oral surface; and by the smaller combed areas.

The type species was confused with *Arachnoides placenta* for many years. To date, it has been authentically recorded only from New Zealand, although it has been listed from Tasmania and Queensland. Mortensen (1948, p. 149) thinks that these two records are probably due to erroneous labels and believes that records from areas other than New Zealand cannot be relied upon until new material is collected.

The type species is strictly littoral, according to Mortensen. It has been recorded (Fell, 1953, p. 247) from the Pliocene of New Zealand.

Subfamily Ammotrophinae n. subfam.

Arachnoididae Gregory, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 132 (in part).

Type genus: *Ammotrophus* H. L. Clark.

Periproct inframarginal in most species; combed areas small; internal supports in an inner ring around lantern as well as in outer marginal zone; ambulacral food grooves extending to apical system in most species.

Miocene to Recent, South Australia and Tasmania.

This subfamily differs from the Arachnoidinae not only in its geographical distribution but in its habitat, which—at least in the Recent species—is deeper. The additional internal supports and the position of the periproct are more specialized than in the Arachnoidinae, but the smaller combed area is less specialized.

Genus *Ammotrophus* H. L. Clark

Ammotrophus H. L. Clark, 1928, Rec. S. Austral. Mus., vol. 3, p. 471; Mortensen, 1948 Mon. Echin., vol. 4, pt. 2, pp. 150–152.

Hesperaster H. L. Clark, 1938, Mem. Mus. Comp. Zool. Harvard Coll., vol. 55, p. 411.

Type species: of *Ammotrophus*, *A. cyclius* H. L. Clark, orig. desig.; of *Hesperaster*, *H. arachnoides* H. L. Clark, orig. desig.

(Fig. 29, c)

Petals wide open; combed areas of ambulacra much reduced, confined to area adjacent to food grooves on aboral surface and to small triangular areas on oral surface; periproct on oral surface, one-third distance from margin; no groove from periproct to peristome; oral surface with a single pair of ambulacral plates meeting across ambulacral suture; interambulacra on oral surface with four post-basicoronal plates in columns 1a, 2b, 3a, and 4b, three plates in columns 1b, 2a, 3b, 4a, 5a, and 5b; periproct in center of first pair of post-basicoronal plates; basicoronal interambulacral plates apparently only slightly larger than ambulacral plates; about twelve aboral plates in each interambulacral column.

According to the information and discussion given by Mortensen (1948, p. 151), it appears that the genus *Hesperaster* is a synonym of *Ammotrophus*, with the possibility existing that *H. arachnoides* is a synonym of *A. cyclius*.

The genus is represented by two or three species from South Australia, from depths of 20 to 45 meters, and the fossil ("Quaternary") *Hesperaster crassus* H. L. Clark from Rottnest Island, Western Australia.

Genus *Monostychia* Laube

Monostychia Laube, 1869, Sitzber. Akad. Wiss. Wien, Math.-naturw. Kl., vol. 59, p. 188; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 315; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 154-155.

Type species: Monostychia australis Laube, monotypic.

(Fig. 29, d)

Test somewhat similar to that of *Ammotrophus*, either polygonal or oblong; ambitus with prominent ambulacral indentations; apical system slightly elevated; ambulacral food grooves extending to apical system, with adjacent areas of test also depressed; no groove from periproct to peristome; combed areas present on ambulacral plates, relatively small and often poorly defined; petals short and open; periproct immediately submarginal; only one pair of ambulacral plates meeting across interambulacral suture; two post-basicoronal plates in each interambulacral column on oral surface; periproct between second pair of post-basicoronal interambulacral plates; basicoronal interambulacral plates about same size as adjacent ambulacral plates; internal supports concentric in marginal areas and radial toward center of test as in *Ammotrophus*. Miocene, South Australia and Tasmania.

The genus is recorded from southern Australia and Tasmania, according to H. L. Clark (1946, pp. 338-339). At least four specific names (*australis* Laube, *loveni* and *elongatus* Duncan, and *Micraster etheridgei* Johnston) have been proposed for taxa within this genus, but Clark believes that only two species are represented. *Arachnoides incisa* Tate (1893) might also be a *Monostychia*. Although some of the occurrences have been called Oligocene by early investigators, it appears probable that in modern terminology they are all of Miocene age (see Fell, 1953, pp. 246-247). The fewer interambulacral plates on the oral surface, the submarginal periproct, and marginal indentations separate this genus from *Ammotrophus*.

Genus *Scutellinoides* n. gen.

Type species: Scutellina patella Tate (1891) = *Scutellina morgani* Cotteau (1891), not *S. patella* Tate of Hall (1908).

Externally similar to *Scutellina* except for supramarginal periproct; apical surface depressed conical; oral surface slightly concave; margin moderately thin, rounded; petals moderately well developed, extending nearly three-fourths distance to margin, somewhat open; pores rounded, not conjugated; apical system and peristome central; periproct supramarginal, distant about two pairs of plates from ambitus; basicoronal interambulacral plates apparently small; interambulacral areas not connecting on oral surface.

Miocene, Australia.

Examination of specimens from the Tate Collection shows that this species has separate auricles, marginal concentric supports, and an inner group of radial interambulacral supports, characteristics which clearly indicate that it is a member of the arachnoidid subfamily Ammotrophinae rather than the Fibulariidae. Its supramarginal periproct is distinctive within this group. In the available specimens it cannot be determined for certain whether there are any post-basicoronal interambulacral plates on the oral surface, but the interambulacra do not

appear to pass onto the oral surface. On the oral surface they are separated by at least one and perhaps two or more pairs of enlarged ambulacral plates. The peripheral concentric supports are not as extensively developed as in *Ammotrophus*, but the inner radial supports are. The combed areas are certainly not well developed, but on the oral surface there are a few oblique rows of secondary tube-foot pores that may represent the combs. The primary tubercles are well developed, prominent, and perforate.

Examination of specimens in the British Museum (Natural History) of the species with a marsupium described by Hall (1908), and referred to *Scutellina patella* Tate, shows that they represent a distinct species which Lambert and Thiéry (1925, p. 577) named *Fossulaster halli* and for which they proposed the genus *Fossulaster*. Hall's species differs from Tate's in that its shape is more elongate, it has internally only two pairs of inner radial supports rather than five pairs, and the female has a marsupium.

Subfamily *incertae cedis*

Genus *Fossulaster* Lambert and Thiéry

Fossulaster Lambert and Thiéry, 1925, Ess. nomencl. rais., p. 577.

Type species: *Fossulaster halli* Lambert and Thiéry = *Scutellina patella* Tate of Hall (1908), not *S. patella* Tate, orig. desig.

(Fig. 38, *a* and *b*)

Outline ovate, oral surface flattened, periproct supramarginal, petals inconspicuous; apical surface of males slightly raised, that of females considerably raised, with highest point anterior to apical system; oral surface of females with well-developed marsupium anterior to peristome; top wall of marsupium nearly touching upper surface of test and causing anterior elevation of apical surface; marsupium with slightly raised longitudinal median partition; 4 genital pores; internal marginal concentric supports moderately developed; only 2 pairs of inner radial supports, posterior pair close together, between periproct and peristome, anterior pair farther apart; basicoronal interambulacral plates not visible on inner surface; auricles separate, small, poorly developed; interambulacra not continuous on oral surface.

Lower Miocene (?), Australia.

Mortensen (1948, p. 230) reported that an unsuccessful search had been made for Hall's specimens and expressed doubt that an oral marsupium was present in this species. However, six specimens, presented by Hall in 1909, are in the British Museum (Natural History). There are four females and two males in the lot. The females, although less well preserved than the males, show a well-defined natural depression (fig. 38, *b*) exactly as described and figured by Hall. There is no doubt that the depression is an original structure and not a malformation. Although the genital pores are clearly evident on the single male with the apical system preserved, they cannot be recognized on any of the females. Unless by some rare chance the anterior genital pores open into the marsupium, it is difficult to see how eggs or larva could be transferred to it. If the structure is not a marsupium, it is difficult to imagine what purpose it serves.

There is no clear trace of the petals on any of the six specimens. The surface of the test is heavily set with fairly large and deeply scrobiculate tubercles. There is a single hydropore in the madreporite, which is covered by small primary tubercles. The plates cannot be clearly recognized on the aboral surface of any of

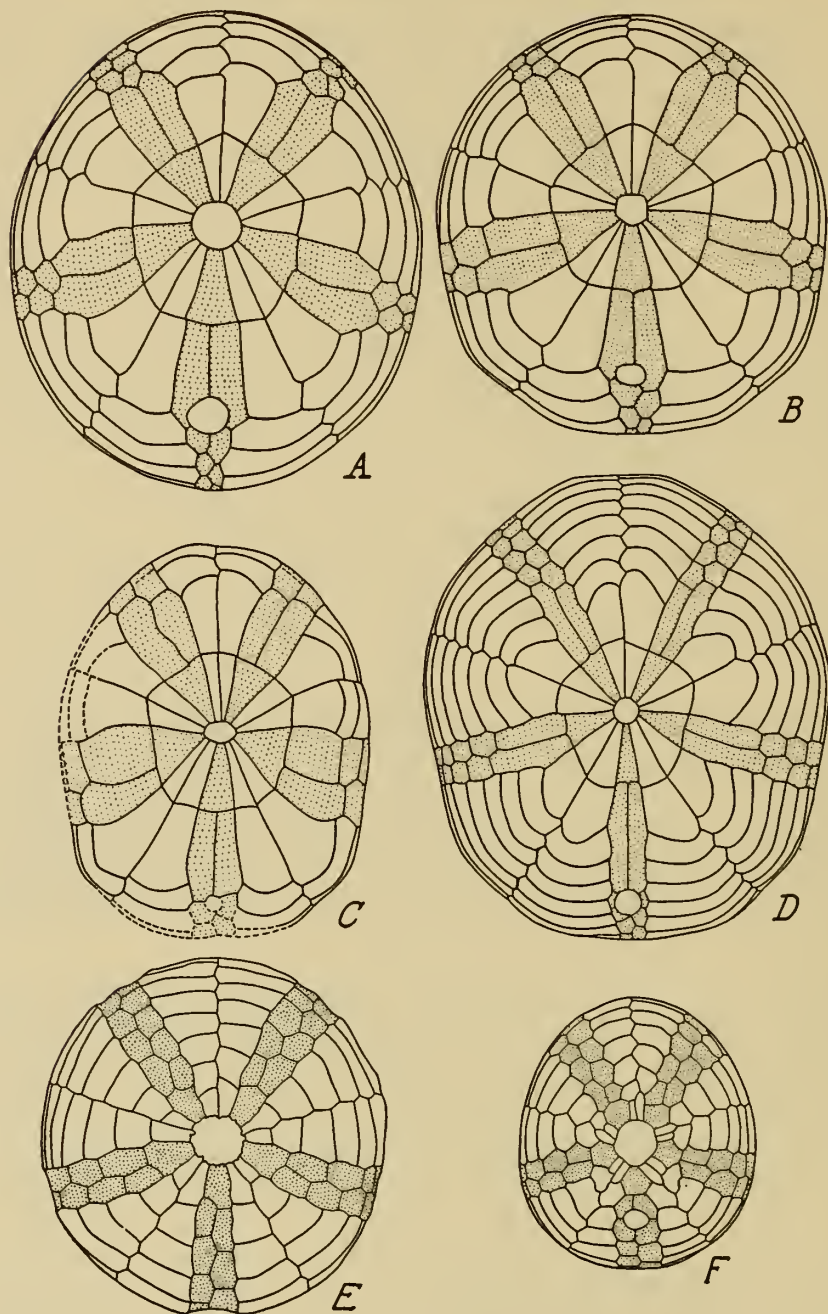


Fig. 30. Structure of oral surface of clypeasteroid echinoids: *a*, *Weisbordella caribbeana* (Weisbord), $\times 1.9$, oral view, hypotype Sanchez Roig Collection; upper Eocene, Cuba. *b*, *Neolaganum archerensis* (Twitchell), $\times 2.25$, oral view, hypotype no. 33296; upper Eocene, Florida. *c*, *Neorumphia elegans* (Sanchez Roig), $\times 0.62$, in part restored, oral view, hypotype Sanchez Roig Collection; upper Oligocene, Cuba. *d*, *Cubanaster torrei* (Lambert), $\times 1.7$, oral view, hypotype no. 33297; upper Eocene, Panama. *e*, *Scutellina lenticularis* Lamarek, $\times 5.4$, oral view, hypotype no. 33845; Lutétian, France. *f*, *Echinocyamus pusillus* (Müller), $\times 6.0$, oral view, hypotype no. 34049; Recent, northern coast of France.

the specimens, but on one female there is a suggestion that there may not be any demiplates in the petaloid part of the ambulacra.

No type specimen for *Fossulaster halli* was designated by Lambert and Thiéry. One (fig. 38, *b*) of the British Museum (Natural History) specimens (no. E 9864) compares favorably with Hall's (1908, p. 140) figure showing the marsupium, and since these specimens are presumably part of the original lot, it is here designated the lectotype of the species. The remaining five specimens (nos. E 9865—E 9869) are designated paratypes.

The presence of only two pairs of inner radial supports makes it difficult to assign this genus to either of the subfamilies of Arachnoididae here recognized. If demiplates actually are missing from the petals, then the suborder Clypeasterina and the family Arachnoididae need to be redefined, for all recognizable characters indicate that this species is an arachnoidid.

Suborder LAGANINA Desor, emended

Tribu des Laganés Desor, 1858, Synop. des échin. foss., p. 217 (in part).

Laganiens Dujardin and Hupé, 1862, Hist. nat. des zooph. échinod., p. 556.

Laganidae A. Agassiz, 1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 516; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 156; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 310.

Proscutidae Lambert, 1899, Bull. Soc. Sci. Yonne, vol. 53, p. 49.

Eoscutidae Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 287.

Laganina Desor, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 156.

Test flattened or inflated, with internal supports when flattened; petaloid ambulacral plates simple or "compound"; interambulacra narrow, continuous, terminated adapically by a single plate (fig. 12, *b*, *d*, *e*); apices of apical system opposite interambulacra; auricles fused; aboral miliary spines with terminal crown (fig. 6, *f-h*); usually no spicules in tube feet.

Senonian to Recent, world-wide, but mostly tropical.

The narrow interambulacra terminated adapically next to the genital plate by a single plate, instead of two plates, are a striking feature of this suborder. In the genus *Tarphypygus* (fig. 12, *e*) from the Eocene of Jamaica and Cuba, a single column of plates begins about midway on the aboral surface and continues to the head of the area. Although no specimens of the Cretaceous species of *Echinocyamus* and *Fibularia* have been examined, it is presumed from their similarity to Cenozoic species that they also have this character. The numerous Eocene species examined all have this feature. This single plate at the head of the interambulacra is a highly specialized feature and thus precludes the derivation of the Clypeasterina and Scutellina from the earlier Laganina. The lack of internal supports or ridges in some, at least, of the fibulariids seems to preclude derivation of the Laganina from *Discoidea* or *Camerogalerus*.

Family Fibulariidae Gray

Fistularina Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 27 (Fibularina in systematic index).

Fibularina A. Agassiz, 1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 505.

Les Fibularidés Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 72.

Fibulariidae Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 144 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 156.

Famille des Scutellinidées Cotteau, 1891, Paléont. Franc., ser. 1, Terr. Tert., vol. 2, p. 303.

Famille des Fibularidées Cotteau, 1892, Paléont. Franc., ser. 1, Terr. Tert., vol. 2, p. 385.

Echinoeyamidae Lambert, 1899, Bull. Soc. Sci. Yonne, vol. 53, p. 49; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 287.

Fibularidae Gray, Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 289 (in part).

Lenitinae Lambert, Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 289; Lambert, 1915, Actes Soc. Linn. Bordeaux, vol. 69, p. 27.

Echinoeyamidae Cooke, 1942, Jour. Paleont., vol. 16, p. 27.

Small, inflated to flattened echinoids, shape variable; petals variable, often indistinct, open; ambulacral food grooves usually absent, indistinct when present; pores in petals rounded (fig. 1, *e*), outer pore not elongate, not conjugate; internal supports of radial partitions only or absent; primordial basicoronal plates not specialized (fig. 14, *a* and *b*).

Senonian to Recent, world-wide.

Members of this family vary greatly in shape, from flattened to highly ovate. The presence of internal supports seems to be correlated with the shape, the ovate *Fibularia* usually lacking supports. The supports are all radially arranged partitions and may be either ten or fifteen in number. They begin at the margin and extend inward a variable distance. When there are only ten supports, they occur at the margins of the interambulacra, when there are fifteen, the additional wall occurs midway between the other two. The lack of internal supports in the ovate species seems to be a primitive character correlated with the shape. The lack of ambulacral food grooves in most species is also a primitive character, as are the relatively undifferentiated basicoronal primordial plates.

The fused auricles and single plate at the head of the interambulacra are highly specialized characters.

Genus *Fibularia* Lamarek

Fibularia Lamarek, 1815, Hist. nat. anim. sans vert., vol. 3, p. 16 (in part); L. Agassiz, 1835, Mém. Soc. Sci. Nat. Neuchatel, vol. 1, pp. 186-187 (in part); L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 142; A. Agassiz, 1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 506 (in part); Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 73; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 146 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 203. Not Lambert, 1891; Lambert and Thiéry, 1914.

Echinocyamus Leske, Gray, 1825, Ann. Philos., n.s., vol. 10, p. 428 (in part); Desor, 1858, Synop. des échin. foss., pp. 220-221; not Leske, 1778; L. Agassiz, 1841; L. Agassiz and Desor, 1847; Desor, 1858; A. Agassiz, 1873; Pomel, 1884; Duncan, 1889; Mortensen, 1948.

Echinocyamus van Phelsum, Lambert, 1891, Bull. Soc. Géol. France, ser. 3, vol. 19, pp. 749-752; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 287.

Type species: Fibularia ovulum Lamarek, by action of Thirteenth International Congress of Zoology, Paris, 1948 (Bull. Zool. Nomencl., vol. 4, p. 519).

(Figs. 5, *d*; 6, *g*)

Moderately small, inflated ovate; petals open, pores not conjugate; periproct usually rounded, on oral surface close to peristome; peristome rounded; no internal supports or walls; hydropores in a groove; buccal membrane naked; 5 large periproctal plates; tube feet without calcareous disc.

Upper Senonian to Recent, world-wide as fossil, living only in Indo-Pacific.

Because no specimens of the type species have been available for study, the above diagnosis is based on the literature. From what can be seen in various illustrations, it appears highly probable that the plate arrangement on the oral surface is very similar to that of *Echinocyamus*. The Upper Cretaceous species ought to be examined critically to determine whether or not the interambulacra have a single plate at the head of each area, and whether or not there are internal sup-

ports. If the periproct has the same advanced position with respect to the peristome in the fossil species as in the type species, it seems highly improbable that this genus is the ancestor of other less specialized fibulariid genera. Genera such as *Porpitella* and *Eoscutum*, which have a supramarginal periproct (in *Porpitella hayesiana* distant about eleven pairs of plates from peristome), are much more primitive than *Fibularia*.

Genus *Fibulariella* Mortensen

Fibulariella Mortensen, 1948, Vidensk. Medd. Dansk. naturh. Foren., vol. 111, p. 72; 1948, Mon. Echin., vol. 4, pt. 2, p. 219.

Type species: Fibularia acuta Yoshiwara, orig. design.

Similar to *Fibularia* but differs from it in having the periproct usually elongate; hydropores not in groove; periproct covered by many small plates; calcareous disc in tube feet; buccal membrane covered by numerous small plates.

Recent, Indo-Pacific.

This genus would be difficult to differentiate from *Fibularia* in the fossil state. However, if well-preserved material is available, the scattered hydropores not in a groove and the elongate periproct should be recognizable.

Genus *Echinocyamus* van Phelsum

Echinocyamus van Phelsum, 1774, Brief aan Cornelius Nozeman over de Gewelw-Slekken of Zee-Egelen, pp. 131–136, pl. 1, figs. 1–35, pl. 2, figs. 1–35 (Explicatio Tabulae); Leske, 1778, Add. ad Klein, p. 213; Gray, 1825, Ann. Philos., n.s., vol. 10, p. 428 (in part); L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, p. 125; L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 140 (in part); Desor, 1858, Synop. des échin. foss., p. 217 (in part); A. Agassiz, 1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 505; Pomel, 1883, Class. méthod. et gén. echin. viv. et foss., p. 73; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 144; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 170–171. Not Lambert, 1891; Lambert and Thiéry, 1914.

Fibularia Lamareck, 1815, Hist. nat. anim. sans vert., vol. 3, p. 16 (in part); L. Agassiz, 1835, Mém. Soc. Sci. Nat. Neuchâtel, vol. 1, pp. 186–187 (in part); Lambert, 1891, Bull. Soc. Géol. France, ser. 3, vol. 19, p. 749–752; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 289. Not L. Agassiz and Desor, 1847; A. Agassiz, 1873; Pomel, 1883; Duncan, 1889; Mortensen, 1948.

Anaster Sismonda, 1841, Mem. R. Accad. Torino, ser. 2, vol. 4, p. 45.

Type species: Echinocyamus pusillus (Müller) = *Spatagus pusillus* Müller, by action of Thirteenth International Congress of Zoology, Paris, 1948 (Bull. Zool. Nomencl., vol. 4, p. 519); of *Anaster*, *A. studeri* Sismonda, monotypic.

(Figs. 8, *k*; 9, *b*, *i*; 14, *a*; 30, *f*)

Small, elongate to rounded, moderately flattened to somewhat inflated; oral surface flat to concave around peristome; petals wide open, sometimes poorly defined; pore-pairs of petals usually oblique, not conjugate; genital and ocular plates fused; apical system central; hydropores few in number, often only one, not in a groove; peristome central; buccal membrane naked; periproct close to peristome, situated at junction between first and second pair of post-basical plates, usually covered by several large naked plates and at times some additional small plates; no spicules in tube feet; 5 pairs of internal radiating partitions.

Senonian to Recent, world-wide as fossil, living in European and Indo-Pacific seas.

Lambert (1891) considered van Phelsum's illustrations to represent a *Fibularia* despite the fact that van Phelsum listed the Adriatic as one of the areas from which his specimens came (there is no living *Fibularia* in the Mediterranean area). This

interpretation of Lambert has produced an unfortunate situation in the literature: most species referred to the genera *Fibularia* and *Echinocyamus* between 1891 and 1948 will have to be reexamined for correct generic allocation.

The more or less flattened test, oral periproct, and ten internal partitions are characteristic of the genus.

Echinocyamus terminalis Grant and Hertlein (1938, pp. 48-49) is a young *Dendraster*. The arrangement of the plates on the oral surface is characteristic of the latter genus in the immature stages. No other eastern Pacific species has been recorded.

The *Echinocentrotus* Checchia-Rispoli cited by Lambert and Thiéry (1914, p. 290) in the synonymy of their *Fibularia* appears to be a purely typographical error in the preparation of the explanation of Checchia-Rispoli's plate. It is not used in Checchia-Rispoli's text, and *Echinocyamus* is used in the explanation of the next figure after the use of *Echinocentrotus*.

Genus *Mortonia* Gray

Mortonia Gray, 1852, Proc. Zool. Soc. London 1851, vol. 19, p. 38; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 73; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 288; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 196-197. Not *Mortonia* Desor, 1858 (= *Mortonella* Pomel, 1883).

Fibularia Lamareck, A. Agassiz, 1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 506 (in part); Tenison-Woods, 1878, Proc. Linn. Soc. N.S.W., vol. 2, p. 168 (in part); Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 146 (in part).

Type species: Mortonia australis (Des Moulins) = *Fibularia australis* Des Moulins, monotypic.

(Figs. 1, *e*; 5, *c*; 6, *h*; 26, *g*; 28, *c*)

Test flattened ovate, concave around peristome, similar to *Echinocyamus*; petals open, well defined, a ridge between members of pore-pairs; peristome central, pentagonal; periproct close to peristome, transversely ovate, situated between first and second pair of post-basicoronal plates; periproct covered by small irregular plates carrying spines; basicoronal plates not specialized, similar to *Echinocyamus*; 6 or 7 pairs post-basicoronal ambulacral plates visible on oral surface; madreporite with a single hydropore; a single posterior pair of partitions only in type species.

Recent, central Pacific.

Contrary to Mortensen's statement (1948, p. 198 and fig. 115, *a*) about the pore-pairs "bending somewhat outward distally," the available material (from Hawaii) shows that the inclination of the pair (in the five available specimens) is distally toward the mid-line of the petal. When the pores are examined, especially from the interior of the test, the outer pore is seen to be inclined apically and the inner pore peripherally as they pass through the wall of the test. Thus, on the outer surface, the outer pore is nearer the apical system than the inner pore. Mortensen's conclusion that the pores are faintly conjugate cannot be verified.

A notable feature on the type species is the ridge between the members of the pore-pairs. It is also supposed to occur on *Echinocyamus polyporus* Mortensen, a species which Mortensen refers to *Mortonia* but which has faint partition walls in the other four interambulacral areas. This species needs to be carefully studied before its assignment to this genus is accepted.

Genus *Thagastea* Pomel

Thagastea Pomel, 1888, Compt. rend. Acad. Sci. (Paris), vol. 106, pp. 373-374; Cotteau, 1892, Paléont. Franc., ser. 1, Terr. Tert., vol. 2, pp. 386-387; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 288; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 225-227.

Thegaster Pomel, Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 294, 305 (misprint for *Thagastea*).

Type species: *Thagastea wetterlei* Pomel, orig. desig.

Test moderately small, somewhat similar to *Fibularia* but with flattened oral surface and subconical apically; very slightly concave around peristome; petals open, well defined, pore-pairs not inclined; several hydropores; peristome central; periproct on oral surface, close to peristome, situated between second and third pair of post-basicoconal plates; no internal supports; interambulacra terminated adapically by a single series of 3 or 4 plates rather than paired plates.

Eocene, Europe and northern Africa.

Cotteau and others have referred to the occasional occurrence of an anterior ambulacral furrow, but it is not present on any of the ten specimens examined.

The adapical series of single plates, rather than a single plate, is similar to, but not as accentuated as, the condition in *Tarphypygyus*. Whether or not this occurs in the type of *Fibularia* is unknown. Cotteau's illustrations (1892, pl. 294, figs. 2, 4; pl. 295, figs. 4, 10) of *T. wetterlei*, showing two columns of plates at the head of the interambulacra, do not agree with the available specimens. The subconical aboral surface and series of single plates in the interambulacra seem to be characteristic.

Genus *Togocyamus* Oppenheim

Togocyamus Oppenheim, 1915, Beitr. Geol. Erforsch. deutschen Schutzgebiete, Heft 12, p. 20; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 228.

Eoscutum Lambert and Thiéry, Cox, 1952, Gold Coast Geol. Surv. Bull. 17, p. 35 (in part); not Lambert and Thiéry, 1914.

Type species: *Echinocyamus (Togocyamus) seefriedi* Oppenheim, monotypic.

Very small, 4 mm. or less; shape similar to *Fibularia*, peristome in a depression; petals open; pore-pairs simple, pores rounded; periproct supramarginal, small; 10 internal partitions; no ambulacral food grooves.

Paleocene, Gold Coast and Togoland, French West Africa.

Because of the supramarginal periproct and internal partitions, Cox (1952, p. 35) referred the type species to *Eoscutum* Lambert and Thiéry. However, *Porpitella doncieuxi* Lambert, the type species of *Eoscutum* is a highly flattened species with partially closed petals and does not appear to be at all closely related to *Togocyamus seefriedi* (Oppenheim). The supramarginal periproct and inflated shape indicate that it is a primitive member of the Fibulariidae. This seems to be the oldest known clypeasteroid echinoid other than the three late Upper Cretaceous species noted elsewhere.

Several specimens of the type species are available in the British Museum (Natural History) but none shows the plate structure. The internal partitions are quite well developed.

Genus *Cyamidia* Lambert and Thiéry

Cyamidia Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 288; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 227.

Type species: *Echinocyamus nummultica* Duncan and Sladen, orig. desig.

Small, variably inflated, similar to *Echinocyamus*, at times flattened; petals well defined, open, inner member of pore-pair smaller than outer; oral surface somewhat flattened; peristome central; periproct midway on oral surface, radially elongate; a single hydropore.

Eocene, India.

Several specimens were examined in the British Museum (Natural History). The shape is quite variable. The elongate periproct and small inner pore seem characteristic. The most common variety is similar in shape to *Echinocyamus*.

Genus *Scutellina* L. Agassiz

Scutellina L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, pp. 98–99; L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 139; Desor, 1858, Synop. des échin. foss., p. 223; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 72; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 145; Cotteau, 1892, Paléont. Franc., ser. 1, Terr. Tert., vol. 2, p. 305–306 (in part); Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 292; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 229–230.

Type species: Scutellina nummularia L. Agassiz = *Scutella nummularia* Defrance = *Scutella lenticularis* Lamarck, orig. desig.

(Fig. 30, e)

Moderately small, flattened, outline circular, margin thin; petals well defined; anterior petal wide open, posterior petals with tendency to close; peristome central; periproct marginal; interambulacra about one-fourth as wide as ambulacra at ambitus; basicoronal plates moderately large, primitive in character, interambulacral plates somewhat larger than adjacent ambulacral plates; anterior interambulacra with 4 or 5 post-basicoronal plates to a column on oral surface, posterior interambulacra with 3 or 4 post-basicoronal plates on oral surface.

Eocene, Europe, northern Africa.

Scutellina patella Tate from the Miocene of Australia has paired instead of fused auricles and internal concentric and radial supports and thus is obviously not a *Scutellina*. The pattern of the plates on the oral surface, together with the above-noted characters, indicate that it is an arachnoidid.

The marginal periproct, small size, relatively small number of oral interambulacral plates, and lack of ambulacral food grooves make *Scutellina* easily recognized.

Genus *Porpitella* Pomel

Porpitella Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 72; Lambert, 1905, Ann. Univ. Lyon, n.s., vol. 17, p. 136–138; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 294; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 231–232.

Scutellina L. Agassiz, Cotteau, 1892, Paléont. Franc., ser. 1, Terr. Tert., vol. 2, pp. 305–306 (in part).

Type species: Scutellina hayesiana L. Agassiz = *S. supera* L. Agassiz = *Cassidulus Hayesianus* Des Moulins, subs. desig., Lambert, 1905.

Small, irregularly ovoid; test slightly arched along longitudinal axis; petals well developed, moderately open, extending nearly to ambitus; apical system and peristome central; periproct supramarginal, about four pairs of plates between it and margin; oral surface arched; interambulacra with 6 or 7 post-basicoronal plates to a column on oral surface; ambulacra with about eight post-basicoronal plates to a column on oral surface; 15 internal radiating partitions.

Eocene, Europe.

Porpitella micra H. L. Clark from the Eocene of Alabama has only ten internal partitions, and the periproct is nearer to the margin than in *Porpitella*. Perhaps it may be referable to *Eoscutum*.

No specimens have been available for examination. Most of the data given above are from Cotteau's figures. There are about ten plates between the periproct and the basicoronal plates, a characteristic which makes this a very primitive genus. The genus is easily recognized by the position of the periproct and the fifteen internal partitions.

Genus *Eoscutum* Lambert

Eoscutum Lambert, Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 293; Lambert, 1915, Actes Soc. Linn. Bordeaux, vol. 69, p. 27; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 230-231.

Type species: Porpitella doncieuxi Lambert, orig. desig.

Small, flattened, apical system somewhat raised; petals well developed, nearly closed, extending slightly more than half distance to margin; periproct just supramarginal; 10 internal radiating partitions.

Eocene, Europe.

No specimen of the type species has been available for study. The nearly closed petals and suggestion of ambulacral food grooves indicate the possibility that this may actually be a young scutellinid echinoid rather than a fibulariid.

Scutellina calvimontanum Cotteau, which has been referred to *Eoscutum*, has open petals extending nearly to the margin. It seems highly improbable that it belongs in this genus.

If a fibulariid, the short, nearly closed petals are characteristic.

Genus *Lenita* Desor

Lenita Desor, L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, Zool., vol. 7, p. 142; Desor, 1858, Synop. des échin. foss. pp. 222-223; Pomel, 1883, Class. method. et gén. échin. viv. et foss., p. 73; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 163; Cotteau, 1892, Paléont. Franc., ser. 1, Terr. Tert., vol. 2, p. 378-379; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 289; Grant and Hertlein, 1938, Univ. of Calif. L. A. Publ. Math. Phys. Sci., vol. 2, p. 49; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 232-233.

Type species: Lenita patellaris Desor = *Echinus patellaris* Gmelin (1791) = *Echinites patellaris* Leske (1778), subs. desig., Desor, 1858.

Small, flattened elliptical, slightly arched along longitudinal axis; petals moderately well developed, open, extending nearly to margin; periproct supramarginal, 1 or 2 plates between it and ambitus; oral surface with a broad longitudinal area without tubercles, lateral margins with longitudinal zone of large tubercles with sunken areoles; small tubercles only on aboral surface; 10 well-developed internal radial partitions, with 5 additional less well developed in a median interambulacral position.

Eocene, Europe, North America(?)

The large tubercles with deeply sunken areoles are unique among the scutellinids. They would seem to imply that, as in many of the spatangids, the spines on the oral surface were fairly long and that there were powerful muscles for movement of the spines. The lack of similar tubercles on *Lenita israelskyi* Grant and Hertlein, from the Eocene of California raises considerable doubt of the validity of its generic assignment.

Mortensen, 1948, p. 233, notes that Lambert and Thiéry report only ten radial partitions, but that he has found fourteen in the type species. The available specimens all appear to have fifteen: two principal partitions lateral in position in the interambulacra, with the third, considerably smaller, median in position.

Genus *Tarphypygus* Arnold and H. L. Clark

Tarphypygus Arnold and H. L. Clark, 1927, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 50, p. 42; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 237.

Type species: Tarphypygus ellipticus Arnold and H. L. Clark, orig. desig.

(Figs. 12, *c*; 14, *b*; 28, *a*)

Small to medium-sized, oval to subglobular; petals well defined, open; apical system and peristome central; oral surface slightly concave immediately adjacent to peristome; periproct on oral surface, between first and second pair of post-basicoronal plates; basicoronal plates small, interambulacral plates considerably elongated; interambulacra continuous on oral surface, about seven pairs of post-basicoronal plates visible; ambulacra with about eleven pairs of post-basicoronal plates on oral surface; ambulacra about one and a half times as wide as interambulacra at ambitus; interambulacra terminated adapically by a single series of several plates rather than two columns.

Eocene, Jamaica and Cuba.

The single series of plates (8 or 9 in *T. clarki*, apparently fewer in the type species) terminating the interambulacra is particularly noteworthy of this genus. Well-preserved individuals seem to show faint ambulacral food grooves radiating from the peristome. The serrate sutures noted by Arnold and Clark seem to be an individual trait. They have been noted occasionally in several other genera.

Genus *Fibulaster* Lambert and Thiéry

Crustulina Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 72, not *Crustulina* Menge, 1867.

Fibulaster Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 296.

Sismondia Desor, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 234-235 (in part). Not Desor.

Type species: Sismondia michelini Cotteau, subs. desig., Cotteau, 1892.

Similar in outline to *Scutellina* but with thicker margin, small; 10 internal radiating supports, curved adambulacrally instead of being linear; petals moderately well formed, open, extending nearly to ambitus; pores rounded, not conjugate; apical system and peristome central; periproct submarginal, approximately between sixth and seventh pairs of post-basicoronal plates; 8 or 9 pairs of post-basicoronal ambulacral plates on oral surface.

Eocene, Europe.

In many respects *Fibulaster* is similar to *Scutellina*, but the thicker margin, curved internal supports, and correspondingly lenticular-shaped interambulacra on the oral surface seem to differentiate it.

No specimens have been available for examination.

Family Laganidae Desor, emended

Tribu des Laganes Desor, 1858, Synop. des échin. foss., pp. 216-217 (in part).

Laganiens Dujardin and Hupé, 1862, Hist. nat. des zooph. échinod., p. 556 (in part); Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 69.

Laganidae Desor, A. Agassiz, 1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 516; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 156; Durham, 1954, Jour. Paleont., vol. 28, p. 677.

Laganidees Cotteau, 1891, Paléont. Franc., ser. 1, Terr. Tert., vol. 2, pp. 248-251 (in part).

Laganidae Duncan, Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 310.

Laganidae A. Agassiz, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 238-250.

Test flattened, outline varying from angulated to rounded; internal supports well developed; petals (fig. 1, *c*) well developed, open, outer member of pore-pair slightly elongated, pores usually

conjugate; apical system and peristome central; genital pores 4 or 5; ambulacral food grooves simple (fig. 2, *c*), not reaching margin; interambulacra continuous, very narrow; adapical terminal interambulacral plate (fig. 12, *b*) rhomboidal; basicoronal plates forming well-defined pentameral star (fig. 15, *e*) with ambulacral plates at apices of rays; no abrupt change in size of oral post-basicoronal ambulacral plates; ambulacral plates not "compound" in petals; periproct oral; no spicules in tube feet or internal organs.

Eocene, Europe; Miocene to Recent, Indo-Pacific, tropical seas.

All the New World species formerly referred to the various laganid genera are now referred to a separate family, the Neolaganidae (Durham, 1954). The basicoronal plates in a well-developed pentameral star and simple plates in the petals, as well as the shape of the adapical terminal interambulacral plate, easily differentiate the two families.

The genus *Sismondia* Desor belongs in this family rather than in the Fibulariidae. The specialized basicoronal plates in a star, the conjugate pore-pairs, the incipient concentric internal supports—all indicate that it is a primitive member of this family.

Genus *Laganum* Link

Laganum Link, 1807, Beschr. Natur-Samml. Univ. Rostock, pt. 3, p. 161; L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, pp. 105–107; Desor, 1858, Synop. des échin. foss., p. 227; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 69; Lambert and Thiéry, 1914, Ess. nomencl. rais., pp. 313–314; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 301–308 (in part). *Lagana* Gray, 1825, Ann. Philos., vol. 26, pp. 427–428; Blainville, 1834, Man. d'Actin., p. 214. *Echinodiscus* Breynius, Lambert and Thiéry, 1914, Ess. nomencl. rais., pp. 311–312 (in part). Not Leske, 1778 (see Bull. Zool. Nomencl., vol. 4, p. 535, 1950).

Type species: *Laganum petalodes* Link = *Echinodiscus laganum* Leske, by tautonymy.

(Figs. 1, *c*; 2, *c*; 7, *b*, *e*; 12, *b*; 15, *e*; 31, *f*)

Medium-sized to large, more or less flattened; oral surface flat, apical area slightly raised; petals moderately open, elongate, length about two-thirds corresponding radius; pore-pairs conjugate, outer pore only slightly elongated; apical system central, genital pores 5, hydropores in a groove; periproct about midway on oral surface, radially elongate; peristome central, with more or less indistinct ambulacral food grooves radiating out from it; basicoronal plates moderately large, in a well-defined star, interambulacral plates about as wide as ambulacral plates; first post-basicoronal plates not greatly larger than succeeding plates; a single pair of plates between periproct and basicoronal row; 5 or 6 post-basicoronal interambulacral plates to a column on oral surface; interambulacra much narrower than ambulacra at ambitus.

The position of the periproct, 5 genital pores, and hydropores in a groove are characteristic of *Laganum*.

Eocene, Europe; Miocene to Recent, Indo-Pacific.

Genus *Peronella* Gray

Peronella Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 13; A. Agassiz, 1872–1873, Mem. Mus. Comp. Zool. Harvard Coll., no. 3, pp. 148, 520; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 69; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 312; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 251–259 (in part).

Type species: *Laganum peronii* Agassiz, monotypic.

(Figs. 8, *j*; 31, *e*)

Medium-sized to large, flattened, outline more or less rounded; oral surface flat to somewhat concave, apical area raised; petals moderately open, variably elongate, length about two-thirds corresponding radius; pore-pairs conjugate, outer pore only slightly elongated; apical system

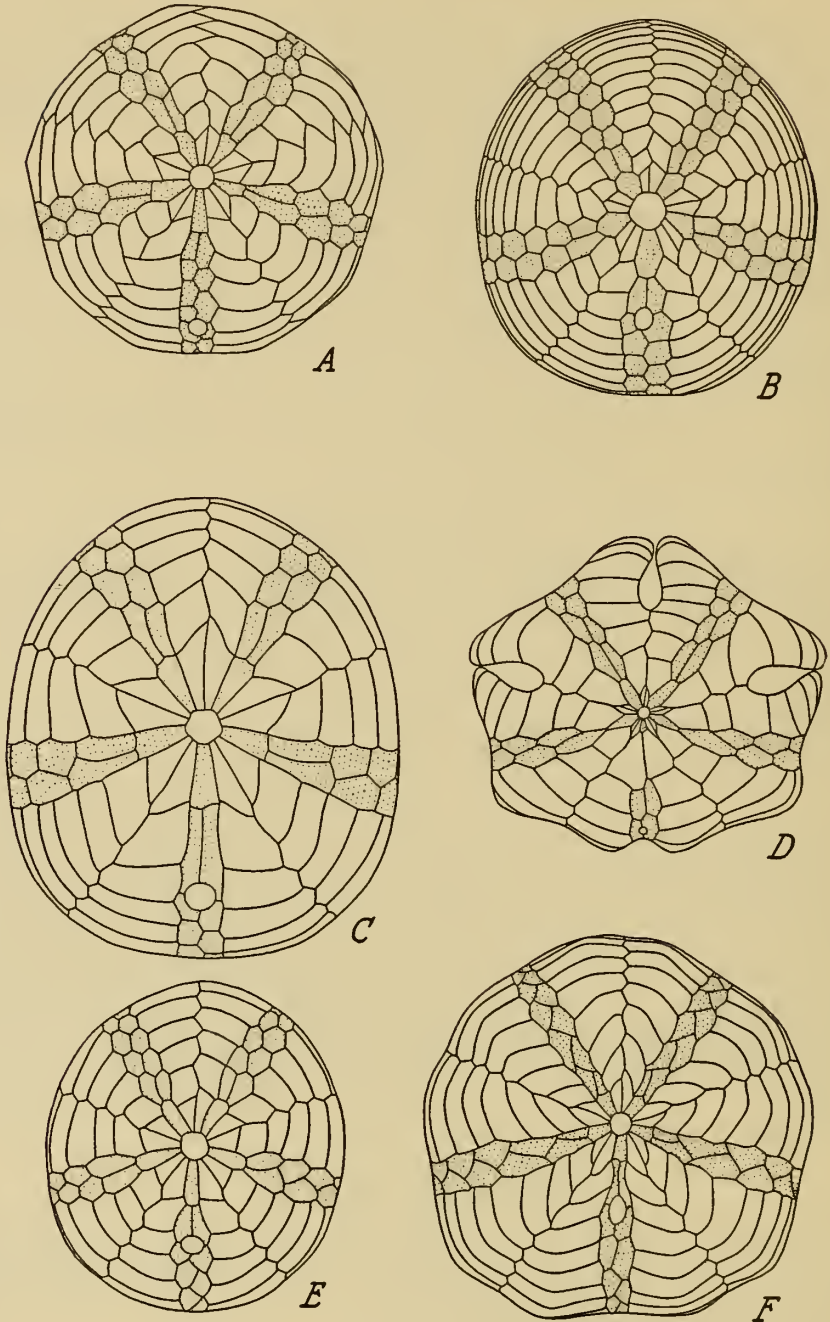


Fig. 31. Structure of oral surface of clypeasteroid echinoids: *a*, *Hupea decagonalis* (Lesson) modified after L. Agassiz (1841, pl. 23, figs. 17, 19); Recent. *b*, *Sismondia occitana* (Defrance), $\times 2.57$, hypotype no. 33762, upper Eocene, France. *c*, *Jacksonaster depressum* (Lesson), $\times 2.5$, Calif. Acad. Sci. hypotype no. 9963; Recent, Philippine Islands. *d*, *Scutaster vaquerosensis* Loel and Corey, $\times 0.57$, composite diagram after holotype no. 31714 and paratype no. 31715 and other specimens; lower Miocene, California. *e*, *Peronella peronii* (L. Agassiz), $\times 1.64$, hypotype Mus. Comp. Zoöl. Harvard Univ., loc. no. 2265; Recent, Australia. *f*, *Laganum laganum* (Leske), $\times 0.87$, hypotype no. 33259; Recent, New Hebrides.

more or less central, genital pores 4, variably situated; hydropores not in a groove; periproct on oral surface, about two-fifths distance from margin; peristome central, with indistinct simple ambulaeral food grooves radiating out from it; basicoronal plates moderately large, ambulaeral plates only slightly larger than interambulaeral plates; first post-basicoronal plates not much larger than the rest; a single pair of plates between basicoronal row and periproct; 4 or 5 post-basicoronal plates to each interambulaeral column on oral surface; interambulaera much narrower than ambulaera at ambitus.

The position of the periproct readily separates *Peronella* from *Rumphia*. The available material has not been adequate to determine whether the genital pores far out from the apical system, as in the type species, should be considered a generic character.

Upper Miocene to Recent, Indo-Pacific.

Genus *Sismondia* Desor

Sismondia Desor, 1858, Synop. des échin. foss., p. 225; Dujardin and Hupé, 1862, Hist. nat. des zooph. échinod., p. 559; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 72; Cotteau, 1891, Paléont. Franc., ser. 1, Terr. Tert., vol. 2, pp. 261-262; Lambert and Thiéry, 1914, Ess. nomencl. rais., pp. 296-297; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 234-236 (in part).

Type species: Scutella occitana Defrance (subs. desig., Pomel, 1883).

(Fig. 31, b)

Small, moderately flattened, margins inflated; oral surface slightly concave, apical system rarely raised; petals moderately open, somewhat lyrate, length about three-fourths corresponding radius; pore-pairs conjugate, outer pore moderately elongate; apical system central, 4 genital pores, hydropores in a groove; periproct about two-fifths distance from margin; peristome central, somewhat pentagonal, in a slight depression; food grooves indistinct; basicoronal plates of moderate size, forming a well-defined star, interambulaeral plates larger than ambulaeral plates; first post-basicoronal plates not much larger than succeeding plates; a single pair of plates between periproct and basicoronal row; about six post-basicoronal interambulaeral plates to a column on oral surface; about eight post-basicoronal ambulaeral plates to a column on oral surface; ambulaera about three times as wide as interambulaera at ambitus.

Eocene, Europe, Africa, and Asia; Oligocene to Miocene, Indo-Pacific, Australia.

The New World species referred to this genus are probably members of the family Neolaganidae. *Sismondia murravica* Tate (fig. 27, e), from the Miocene of Australia has fewer plates on the oral surface than the type species.

Genus *Hupea* Pomel

Hupea Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 69.

Type species: Laganum decagonale Pomel = *Scutella decagonalis* Lesson, orig. desig.

(Figs. 10, b; 26, i; 31, a)

Medium-sized, outline more or less polygonal, flattened; oral surface flat, apical area raised; petals small, slightly open, length about one-half radius of test; pore-pairs conjugate, outer pore slightly elongate; apical system central, 5 genital pores; hydropores not in a groove; periproct submarginal, distant about its own diameter from margin; peristome central, with indistinct simple ambulaeral food grooves radiating from it; basicoronal plates of moderate size, forming a star, ambulaeral plates slightly wider than adjacent interambulaeral plates; first post-basicoronal plates not greatly larger than subsequent plates; 3 pairs of plates between basicoronal row and periproct; 4 or 5 post-basicoronal interambulaeral plates per column on oral surface; interambulaera much narrower than ambulaera at ambitus.

Pliocene, Java; Recent, Malaysian and Polynesian areas.

No specimens have been available for study.

At present only the type species can be referred to the genus. In his text, Pomel does not credit the name *decagonale* to any author, but since he does not describe any species in this paper, and all names cited without author are names which have been used by other authors for species within the genera cited, it must be presumed that he was referring to *Scutella decagonalis* Lesson, which had been well figured and described by L. Agassiz (1841, pl. 23, figs. 16–20) under the name *Laganum decagonum* Lesson. Both Lesson and L. Agassiz clearly indicate that the species they were discussing had five genital pores. However, in 1873, A. Agassiz described and figured as *Laganum (Peronella) decagonalis* Lesson a species with only four genital pores. The species figured by A. Agassiz is considered by Mortensen (1948, pp. 263–264, 271) to be referable to *Peronella lesueuri* (Agassiz) and not to *Scutella decagonale* Lesson.

In his diagnosis of *Hupea*, Pomel states that the genus is characterized by four genital pores, making it seem possible that he was basing his description on the *decagonalis* of A. Agassiz rather than on that of Lesson and L. Agassiz. If this interpretation were correct and Mortensen's statement that *Laganum rostratum*, *L. elongatum*, and *L. lesueuri* are all variants of a single species were also correct, then *Hupea* Pomel, 1884, would be a synonym of *Rumphia* Desor, 1858.

However, inasmuch as *Hupea* Pomel has not been generally recognized by subsequent authors or cited in the literature, and as the species *Laganum decagonale* (Lesson) with five genital pores is not referable to the genus *Laganum* in the sense in which it is used here, it seems desirable to invoke Article 30 of the Rules of Zoological Nomenclature, and Opinions 65 and 168 of the International Commission on Zoological Nomenclature, and consider that *L. decagonale* (Lesson) was correctly identified by Pomel but that he misstated its characters, and that *L. decagonale* (Lesson) as correctly figured and described by L. Agassiz (1841) but not by A. Agassiz (1873) is the type of the genus *Hupea* Pomel.

Genus *Peronellites* Hayasaka and Morishita

Peronellites Hayasaka and Morishita, 1947, Acta Geol. Taiwanica, vol. 1, p. 101; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 257.

Type species: *Peronella (Peronellites) ovalis* Hayasaka and Morishita, monotypic.

No specimens of the type species are available, and the figures and original description are inadequate for comparison. However, the elongate outline, vaulted apical area, and differential petal lengths may be distinctive. The author's diagnosis is as follows: "Test elliptical in outline; genital pores four, wanting in interambulacrum V: apical system and proximal ends of petals markedly vaulted up." The type species has the apical system slightly excentric anteriorly; petals short, not longer than half the radius; the anterior petal longest, and anterior paired petals shortest; poriferous zones "very narrow," interporiferous zones broader. The type species is from the Miocene of Formosa.

Genus *Rumphia* Desor

Rumphia Desor, 1858, Synop. des échin. foss., p. 229; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 69; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 312 (in part).

Polyaster Michelin, 1859, Rev. et Mag. Zool., p. 397, not *Polyaster* Gray, 1840.

Michelinia Dujardin and Hupé, 1862, Hist. nat. des zooph. echinod., pp. 560-561, new name for *Polyaster* Michelin, not *Michelinia* de Koninek, 1842.

Type species: of *Rumphia*, *Laganum rostratum* L. Agassiz, orig. desig.; of *Polyaster*, *Polyaster elegans* Michelin, monotypic.

Medium-sized to large, more or less elongate, flattened; oral surface flat, apical area raised; petals elongate, open, length nearly two-thirds radius of test; pore-pairs conjugate, outer pore slightly elongate; apical system slightly anterior; 4 genital pores, with 2 posterior pores farther apart than anterior pair; hydropores not in a groove; periproct on oral surface, close to margin; peristome of medium size, nearly central, with simple ambulaeral food grooves extending about halfway to margin; basicoronal plates large, forming a pentameral star; interambulaeral areas very narrow on oral surface; precise number of post-basicoronal ambulaeral plates on oral surface uncertain but about seven, gradually decreasing in altitude towards ambitus; number of post-basicoronal interambulaeral plates unknown, but probably 4 or 5.

Miocene to Recent, Indo-Pacific.

No specimens have been available for study; the diagnosis is based on the literature.

Apparently there are very few specimens of *Laganum rostratum* available. Mortensen (1948) figures two specimens which he questionably refers to *rostratum* and then considers it as a variety of *Peronella lesueuri* (L. Agassiz). The data available are inadequate to demonstrate that *L. rostratum*, as figured by L. Agassiz (1841, pl. 25, figs. 1-10), is conspecific with *L. lesueuri* L. Agassiz (1841, pl. 24, figs. 3-6) and *L. elongatum* L. Agassiz (1841, pl. 24, figs. 1 and 2), both of which are commonly considered conspecific, but it appears possible that they are congeneric. *Polyaster elegans* Michelin has been considered by H. L. Clark (1925, p. 160) to be a variety of *Peronella lesueuri* (L. Agassiz). If the preceding species can be shown to be generically separable, a new generic name should be proposed for *Michelinia* Dujardin and Hupé, not de Koninek. From Agassiz's figures, although inadequate for a complete diagnosis, it can be seen that *rostratum*, *lesueuri*, and *elongatum* are not congeneric with *L. peronii*, the type of *Peronella*, or with the types of *Laganum*, *Hupea*, and *Jacksonaster*.

Rumphia may be readily separated from *Peronella* by the periproct close to the margin, and probably by more than one pair of plates between the periproct and the basicoronal row. If *Laganum elongatum* L. Agassiz is congeneric, then there are about four pairs of plates between the periproct and the basicoronal row. If *Laganum lesueuri* is congeneric, the genus is recorded from the Miocene of Java (Jeannet and Martin, 1937, p. 256), and in the Pliocene from several places in the Indo-Australian area.

Genus *Jacksonaster* Lambert and Thiéry

Jacksonaster Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 313; Lambert, 1915, Aetes Soc. Linn. Bordeaux, vol. 79, p. 28, n.

Laganum Klein, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 301-307 (in part).

Type species: *Jacksonaster conchatus* (M'Clelland) = *Echinarachnius conchatus* M'Clelland = *Lagana depressum* Lesson, orig. desig. In the 1915 paper (date given as 1914 in Ess. nomencl. rais., but volume was not published until 1915) the type is stated to be *Laganum depressum* Lesson.

(Figs. 1, *h*; 5, *j*; 7, *a*; 26, *h*; 31, *c*)

Medium-sized to large, flattened; oral surface flat, apical area slightly raised; petals moderately open, length about two-thirds corresponding radius; pore-pairs conjugate, outer pore

slightly elongate; apical system central, genital pores 5; hydropores in a groove; ambulacral food grooves extending slightly more than half distance to margin; periproct about one-fourth distance from margin, often transversely elongate, situated between first and second pair of post-basicoronal plates; in interambulacrum 5 first pair of post-basicoronal plates considerably elongated; basicoronal plates in well-formed star, ambulacral and interambulacral plates about equal; about five ambulacral and 3 or 4 interambulacral post-basicoronal plates on oral surface; interambulacra much narrower than ambulacra at ambitus.

Miocene to Recent, Indo-Pacific.

Jeannet and Martin, (1937, p. 253) record the type species from the upper Miocene of Madoera.

This genus may be differentiated from *Laganum* by the more nearly marginal periproct, the fewer plates on the oral surface, the greatly elongated first pair of post-basicoronal plates in interambulacrum 5, as well as by the differences in shape of the periproct.

It should be noted that the *Laganum depressum* Lesson figured by Lovén (1874, pl. 45, fig. 236) is not correctly identified. There is no groove for the hydropores, there are four genital pores, and there are more plates between the periproct and the basicoronal row. It seems to be more nearly assignable to *Peronella* than to any other genus.

Genus *Fibulina* Tornquist

Fibulina Tornquist, 1904, Abh. senckenb. naturf. Ges., vol. 27, p. 327; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 288; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 227.

Type species: Fibulina gracilis Tornquist, monotypic.

Described as similar to *Fibularia* but with 5 furrows (ambulacral food grooves?) radiating from peristome.

Eocene, Madagascar.

No specimens of the type species are available, and Tornquist's figure is inadequate. Tornquist describes it as having five ambulacral furrows, a concave lower surface, and an inflated margin. From his description, it appears probable that it is a laganid rather than a fibulariid, although he compares it with *Fibularia* and *Thagastea*.

Family Neolaganidae Durham

Neolaganidae Durham, 1954, Jour. Paleont., vol. 28, p. 680.

Laganidae, *auctores* (in part).

Type genus: Neolaganum Durham (1954).

Test flattened, internal radial and concentric supports; ambulacra petaloid aborally; petaloid area usually with "compound" plates (fig. 27, *a-c*); outer member of pore-pairs greatly elongated; interambulacra very narrow, terminated adapically by a single plate only (fig. 12, *d*); oral surface with simple ambulacral food grooves not reaching margin; basicoronal plates in a regular pentagon, with ambulacral plates at apices (fig. 15, *f*); first post-basicoronal ambulacral plates larger than later plates; periproct on oral surface; presence or absence of spicules in internal organs and tube feet unknown; character of aboral miliary spines unknown.

Eocene to Oligocene, Gulf of Mexico to Caribbean area.

Most of the New World species previously referred to genera here placed in the family Laganidae can readily be shown to belong to the family Neolaganidae, but a few of them—perhaps because no specimens have been available for examination—require special consideration. *Jacksonaster chilensis* Lambert and Thiéry

(1914, p. 313, pl. 8, figs. 5-7) from the "Pliocene" of Chile is one of these. The ambulacral food grooves are suggestive of a laganinid echinoid, but the general shape is more characteristic of a species of *Clypeaster* such as *ravenelii* (A. Agassiz), which also has indistinct ambulacral food grooves. Unfortunately, the details of the figure are not adequate to indicate whether it is a *Clypeaster* or a laganinid. If it is a laganinid s. s. it could be a transpacific migrant which did not become permanently established. It is also possible that the species is a neolaganid and that its age is incorrectly determined (all other neolaganids are of Eocene-Oligocene age), but the marked pentagonal outline with the interambulacral margins indented is not like that of any other neolaganid.

The New World species which have been referred to *Sismondia* require more careful consideration. Unfortunately, specimens of only one species have been available for examination. The following species have been referred to *Sismondia* at one time or another: *S. alta* Conrad, 1865, now considered a synonym of *Periarchus lyelli* (Conrad); *S. marginalis* Conrad, 1865, now considered a synonym of *Protoscutella conradi* (Cotteau); *S. plana* Conrad, 1865, now referred to *Protoscutella*; *Scutella crustuloides* Morton, here referred to the Neolaganidae; *Sismondia occitana* DeFrance (Sanchez Roig, 1949, p. 65); *S. aff. crustula* H. L. Clark [Hawkins] (Sanchez Roig, 1949, p. 65); *S. antillarum* (Cotteau, 1875; Jackson, 1922, p. 30, pl. 2, figs. 6 and 7); *S. anguillae* Cotteau (Cotteau, 1875; Jackson, 1922, pp. 30-31, pl. 2, figs. 8 and 9); and *S. crustula* Hawkins (1927, pp. 78-79, pl. 22, figs. 4 and 5). The details of the figures and of the descriptions of *S. occitana* of Sanchez Roig, *S. aff. crustula* of Sanchez Roig, *S. antillarum* Cotteau, and *S. anguillae* Cotteau are not adequate bases for conclusions in regard to the correctness of the generic reference. *S. crustula* Hawkins has two rows of large primary tubercles inside the petals in a manner comparable to that in *Cubanaster torrei* (Lambert). These large primary tubercles indicate the presence of "compound" plates in the petals in the laganinid echinoids and consequently suggest strongly that this species is a neolaganid and probably referable to *Neologanum*. According to Hawkins, *S. antillarum* Cotteau is very similar to *crustula*; consequently it would seem probable that it is a neolaganid also. In view of this it seems best at present to consider that there are no New World species which can be unequivocally assigned to *Sismondia*, and that some, at least, are referable to the family Neolaganidae.

Specimens of several Caribbean-Gulf of Mexico "laganid" species have not been available. Until they have been carefully examined, they are left generically unassigned. These species are: *Laganum floridanum* Twitchell, *L. ocalanum* Cooke, *Scutella crustuloides* Morton, *Laganum johnsoni* Twitchell, *L. elongatum* Egozcue, and *Laganum cubanum* Weisbord.

The Neolaganidae may be readily separated from the Laganidae by the following characters: usually "compound" plates in petals; basicoronal plates arranged in a more or less regular pentagon, not in a pentagonal star; first pair of post-basicoronal plates considerably larger than the remaining plates as contrasted with plates gradually decreasing in altitude; outer member of pore-pairs greatly elongated as contrasted with only slightly elongated; terminal adapical interambulacral plate approximately rectangular (fig. 12, d) as contrasted with rhom-

boidal (fig. 12, b); range Eocene to Oligocene as contrasted with Eocene to Recent (with major expansion in Miocene to Recent); restricted to New World as contrasted with Old World and Indo-Pacific.

Genus *Neolaganum* Durham

Neolaganum Durham, 1954, Jour. Paleont., vol. 28, p. 680.

Type species: Laganum archerensis Twitchell, orig. desig.

(Figs. 15, f; 30, b)

Small to medium-sized, slightly pentagonal, flattened "laganid" echinoids; oral surface flat, apical area slightly raised, upper surface of test very slightly depressed inside margin at end of petals; petals elongate, slightly raised, almost closed, length two-thirds radius of test; pore-pairs conjugate, outer pore elongate; plates within petals "compound," composed of dyads and triads; apical system slightly anterior; 4 genital pores with 2 posterior pores more distally situated than 2 anterior pores; hydropores in a branching groove as in *Laganum*; periproct on oral surface, about one-fourth distance from margin; peristome small, slightly anterior; simple ambulacral food grooves, extending about halfway to margin; basicoronal plates large, forming a pentagon around peristome, ambulacral plates about one-half as wide as adjacent interambulacral plates; first pair of post-basicoronal interambulacral plates elongated, extending nearly to ambitus, 2 or 3 small additional plates between them and ambitus.

This genus is characterized by the rather small number of plates on the oral surface and the groove on the madreporite into which the hydropores open. This groove, the more pentagonal shape, especially posteriorly, and the flat or nearly flat oral surface distinguish this genus from *Weisbordella*.

The presence of the groove in the madreporite in the laganid echinoids has had but little attention, yet according to the present studies it is widely present and significant, being characteristic of *Laganum* but not present in *Peronella*, for instance. It seems to be widely present in the neolaganids, although there are a number of species that have not been examined. The available data seem to indicate that it is at least of generic significance. For instance, on other grounds (flatness of oral surface) Cooke (1942) referred *Laganum archerensis* (with groove) to *Rumphia* Desor, and *Peronella caribbeana* (without groove) to *Peronella* Gray. In the present studies the groove in the madreporite seems to be a more significant difference. If these differences should be found to be of lesser value, *Neolaganum* should have priority over *Weisbordella*.

The type species is from the upper Eocene of the Gulf Coast.

Genus *Cubanaster* Sanchez Roig

Cubanaster Sanchez Roig, 1949, Paleont. Cubana, vol. 1, p. 105 (*nomen nudum*); 1952, Torreia, no. 16; p. 3; Durham, 1954, Jour. Paleont., vol. 28, p. 681.

Type species: Jacksonaster torrei Lambert, orig. desig.

(Figs. 13; 30, d)

Small to medium-sized, more or less ovate, pentagonal, flattened "laganid" echinoids; oral surface flat, aboral surface more or less depressed inside margin; petals approximately flush with surface, elongate, slightly open, length about three-fourths radius of test; pore-pairs conjugate, outer pore greatly elongated; plates within petals partially "compound," with some dyads; apical system slightly anterior; genital pores 4; hydropores in a groove; peristome slightly anterior, rounded; periproct on oral surface, about one-sixth distance from margin;

ambulacral food grooves simple, extending about one-half distance to margin; basicoronal plates large, ambulacrals about equivalent to interambulacrals; first pair of post-basicoronal interambulacral plates elongated, extending about half or more of the post-basicoronal distance on the oral surface, remaining interambulacral plates small; interambulacral areas narrow, about one-fourth width of adjacent ambulacral areas; center of periproct situated at junction of sutures between second and third post-basicoronal plates, but large in comparison to adjacent plates, so that it also comes in contact with first and fourth pair of plates.

Upper Eocene, West Indies, Panama.

This genus is easily separable from the other neolaganids by the large number of plates on the oral surface, the narrow interambulacra on the oral surface, and the elongate petals flush with the aboral surface.

In addition to the type species, *Jacksonaster acunai* Lambert, *J. santanae* Sanchez Roig, *J. depressus* Sanchez Roig, *Cubanaster camagüeyensis* Sanchez Roig, *C. herrerae* Sanchez Roig, *C. sandiegensis* Sanchez Roig, *C. planipetalum* Sanchez Roig, *C. santanae* Sanchez Roig, and perhaps *J. cubensis* Lambert, *J. remediensis* Sanchez Roig, and *J. sandiegensis* Sanchez Roig are to be referred to this genus.

Genus *Neorumphia* Durham

Neorumphia Durham, 1954, Jour. Paleont., vol. 28, p. 681.

Type species: *Rumphia elegans* Sanchez Roig, orig. desig.

(Figs. 27 a; 30, c)

Rather large, elongate, posteriorly truncated, "laganid" echinoids; oral surface slightly concave, aboral surface raised centrally; margin of test moderately thick; petals fairly long, length about three-fourth radius of test, usually slightly pointed, almost closed; petals with plates "compound," mostly triads and tetrads; pore-pairs conjugate, outer pore elongate, pore-pair approximately normal to axis of petal; genital pores 4, just inside reentrants between petals; hydropores apparently in a branching groove; peristome slightly anterior, compressed in an anterior-posterior direction; periproct rounded, large, distant about twice its diameter from margin; basicoronal plates large, all about same length, interambulacral plates about twice as wide as adjacent ambulacrals; first post-basicoronal interambulacral plates considerably elongated, remaining interambulacral plates on oral surface small; interambulacral areas, except 5, about half as wide as ambulacral areas at ambitus, interambulacrum 5 very narrow at ambitus; periproct between second pair of post-basicoronal interambulacral plates.

Upper Oligocene, Cuba.

Laganum lamberti Sanchez Roig and *L. santanae* Sanchez Roig, from the upper Oligocene of Cuba, are other species which appear to be referable to this genus. The "compound" plates within the petals of *L. lamberti* are mostly triads. The plates in the petals of *L. santanae* have not been examined. Contrary to Sanchez Roig's description, the type specimen of *L. lamberti* has only four genital pores. Similarly, a specimen of *L. santanae*, lent by him for examination, also has only four genital pores.

The few plates on the oral surface combined with the elongate oval shape and petals flush with surface are characteristic.

Genus *Sanchezella* Durham

Sanchezella Durham, 1954, Jour. Paleont., vol. 28, p. 682.

Type species: *Jacksonaster sanchezi* Lambert, orig. desig.

(Figs. 12, *d*; 27, *b*; 28, *b*)

Medium-sized, elongate, thickened, "laganid" echinoids; oral surface moderately concave; margins of test thick, rounded; oral surface of test slightly arched in an antero-postero direction; upper surface slightly concave; petals depressed, elongate, open; pore-pairs conjugate, outer pore elongate; petals with occasional dyad plates; apical system slightly anterior; genital pores 4; hydropores in a groove; peristome slightly anterior, rounded; periproct large, rounded, on oral surface with center about one-fourth distance from margin; basicoronal plates large, mostly even, but shorter laterally than in antero-postero direction; first pair of post-basicoronal interambulacral plates elongated, remaining interambulacral plates on oral surface small; interambulacral areas narrow, less than one-fourth width of adjacent ambulacral areas on oral surface but widening rapidly at ambitus; center of periproct situated at junction of sutures between second and third post-basicoronal plates, large as in *Cubanaster*.

Upper Eocene, West Indies.

The elongate outline, thick margin, depressed petals, and large number of post-basicoronal oral ambulacral plates are characteristic.

Genus *Weisbordella* Durham

Weisbordella Durham, 1954, Jour. Paleont., vol. 28, p. 682.

Type species: *Peronella caribbeana* Weisbord, orig. desig.

(Figs. 27, *c*; 30, *a*)

Medium-sized, slightly ovate, "laganid" echinoids; oral surface slightly concave, petaloid area raised, margin of test moderately thin; petals short, broad at base, moderately pointed but slightly open; plates within petals "compound," mostly triads but some dyads; pore-pairs conjugate, outer pore elongate, strongly inclined peripherally from axis of petal; apical system slightly anterior; genital pores 4, inside reentrants between petals; hydropores not in a groove; peristome slightly anterior, rounded; periproct large, rounded, on oral surface, distant its diameter from margin; basicoronal plates large, all about same length, but interambulacral plates nearly twice as wide as adjacent ambulacral plates; first pair of post-basicoronal interambulacral plates elongated, remaining interambulacral plates on oral surface small; interambulacral areas narrow, less than one-fourth width of ambulacral areas at ambitus; periproct situated at suture between first and second pair of post-basicoronal plates.

Upper Eocene, West Indies.

Superficially this genus is very similar to the Indo-Pacific *Peronella* in general shape and in outline of petals. It is also similar to *Neolaganum* but does not have the groove for the hydropores which is present in that genus. According to Cooke (1942, p. 25), *Peronella quinquenodulata* Weisbord and *P. caribbeana* Weisbord are synonyms of *P. cubae* Weisbord. *Laganum dalli* Twitchell and *Peronella mirabilis* Jackson are other species probably belonging to this genus.

Genus *Wythella* Durham

Wythella Durham, 1954, Jour. Paleont., vol. 28, p. 682.

Type species: *Laganum eldridgei* Twitchell, orig. desig.

(Fig. 27, *d*)

Medium-sized to large, more or less pentagonal, flattened "laganid" echinoids; oral surface flat; aboral surface slightly depressed inside margin, moderately raised in center; petals raised adjacent to apical system, length about two-thirds radius, well formed, closed; plates in petals "compound," in triads and dyads; pore-pairs conjugate, outer pore greatly elongated; apical system approximately central; genital pores 4; hydropores in a groove; peristome central,

rounded; periproct on oral surface, about one-fourth distance from margin; ambulacral food grooves simple and distinct for about one-half radius of test; basicoronal plates large, ambulacra about equal to interambulacra; first pair of post-basicoronal ambulacral and interambulacral plates moderately elongated, length about one-third the corresponding radius, later plates successively smaller in altitude; interambulacral areas widen to a maximum width equal to adjacent ambulacral areas at a point slightly more than one-half the distance of the radius from the peristome, then narrow to the ambitus, where they are about one-eighth width of adjacent ambulacra; center of periproct situated about at junction between second and third pairs of post-basicoronal plates, large in comparison to size of plates.

Upper Eocene, Gulf of Mexico area.

This genus is similar to *Cubanaster* Sanchez Roig but differs from it in having thinner margins, raised petals, and wide interambulacral areas about midway on the oral surface. It also resembles *Neorumphia* but has fewer plates on the oral surface, a thinner margin, and narrower interambulacral areas at the ambitus.

The type is the only species now known to be referable to the genus. It occurs in the Ocala limestone, late upper Eocene of the Gulf Coast of the United States.

Suborder SCUTELLINA Gray, emended

Scutellidae Gray, 1825, Ann. Philos., n.s., vol. 10, p. 427 (in part); Gray, 1855, Cat. Rec. Echin.

Brit. Mus., pt. 1, p. 2 (in part); Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 310 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 345-359 (in part).

Des Scutelles L. Agassiz, 1841, Mon. d'Echinod., Sec. Mon., Des Scutelles, pp. 1-6.

Tribu des Scutellides Desor, 1858, Synop. des échin. foss., p. 230.

Scutelliens Dujardin and Hupé, 1862, Hist. nat. des zooph. échinod., p. 562 (in part).

Scutellidae L. Agassiz, A. Agassiz, 1875, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 524 (in part); Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 157 (in part).

Les Scutellides Pomel, 1883, Class. méthode et gén. échin. viv. et foss., p. 68 (in part).

Famille des Scutellidees Cotteau, 1891, Paléont. Franc., ser. 2, Terr. Tert., vol. 2, pp. 236-238 (in part).

Usually flattened; internal supports usually well developed, both concentric and radial; ambulacra petaloid adapically, no "compound" plates in petals; plates of petals much smaller than oral ambulacral plates; pore-pairs conjugate; interambulacra terminating adapically in a pair of plates (fig. 12, *f*), often discontinuous on oral surface in advanced genera; ambulacra as wide as or wider than interambulacra at ambitus; apical system pentagonal or stellate, apices corresponding to interambulacra (fig. 1, *d, i*); peristome central, buccal membrane naked; basicoronal interambulacral plates as large as or larger than ambulacral plates, often greatly developed; auricles fused (fig. 9, *a*); primary spines simple or club-shaped (fig. 5, *a, b, e*); aboral miliary spines terminating in glandular bag (fig. 6, *d* and *e*); ambulacral food grooves present, often highly complicated, with terminal projection extending over buccal tube-feet pores; tube feet with 2 spicules in sucking disc (fig. 8, *a* and *b*).

Eocene to Recent, world-wide.

With the demonstration that the genus *Scutellaster* Cragin is a Pliocene rather than a Cretaceous echinoid (Durham, 1953c), the oldest scutellinid echinoid seems to be the genus *Eoscutella* Grant and Hertlein, which occurs in the lower Eocene (as distinct from Paleocene) of California and Oregon. *Eoscutella* is a highly specialized genus in many respects and obviously is not the ancestor of the later members of the group. The principal scutellinid characters, except separation of the interambulacral areas on the oral surface, are well developed in this genus, which would seem to indicate that there are unrecorded scutellinid echinoids of pre-lower Eocene age. Separation of the interambulacral areas on the

oral surface is a trait that is not seen in the earliest members of the suborder but becomes increasingly common as the present epoch is approached.

Mortensen (1948, p. 356) and others have concluded that the scutellinid echinoids are near relatives of the Laganina, but the presence of a single plate at the head of the interambulaera in the laganinids and the highly advanced position of the periproct in the Upper Cretaceous fibulariids indicate that if the two groups are related, they must be descendants of a pre-upper Senonian ancestor. Otherwise the Scutellina must have a different immediate ancestor from the Laganina.

Gaps in various apparent evolutionary sequences in the suborder seem to indicate, despite the abundant fossil record in the Upper Cenozoic, that there are many different types of scutellinids yet to be found, particularly in the Lower Cenozoic. Records of representatives of the group are notably absent from the New World Oligocene faunal lists, for instance.

The geographic and geologic distribution, together with a careful analysis of relationships, indicates that there are many more distinct suprageneric groups in the suborder than have been previously recognized. These groups are here considered to be families. Some of the families recognized contain only a single genus at present. It is felt that this is warranted because the structure of the test, as well as other characters, indicates that these genera are not closely related to other described genera.

Family Scutellidae Gray, emended

Scutellidae Gray, 1825, Ann. Philos., n.s., vol. 10, p. 427 (in part).

Phelsumasteridae Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 316 (in part).

Scutellinae Lahille, 1896, Rev. Mus. La Plata, vol. 7, pp. 441-442 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 360 (in part).

Medium-sized to large, flattened, with well-developed internal supports; petals closed, no primary pore-pairs outside petals; outer member of pore-pair elongated, subdivided; interambulaera continuous, about same width as ambulaera at ambitus; basicoronal ambulaeral and interambulaeral plates approximately equal (fig. 14, c), large; 4 genital pores; periproct on oral surface; ambulaeral food grooves bifurcating just outside basicoronal plates (fig. 3, c).

Oligocene to Miocene, Europe, Northern Africa.

Genus *Scutella* Lamarek

Scutella Lamarek, 1816, Hist. nat. anim. sans vert., vol. 3, p. 7 (in part); L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, pp. 75-76 (in part); Lambert, 1912, Mem. Soc. Paléont. Suisse, vol. 38, pp. 57-61 (in part); Lambert and Thiéry, 1914, Ess. nomencl. rais., pp. 317-319 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 360-362 (in part); Durham, 1953, Jour. Paleont., vol. 27, pp. 348-349.

† *Lambertiella* Checchia-Rispoli, 1917, Palaeont. Ital., vol. 23, pp. 57-58; Lambert and Thiéry, 1925, Ess. nomencl. rais., p. 581; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 255-256.

† *Peronella* Gray, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 251-259 (in part).

Type species: of *Scutella*, *Scutella subrotunda* Lamarek = *Echinodiscus subrotundus* Leske = *Scutella subrotunda* L. Agassiz (1841) in part (not pl. 17, figs. 1-11 = *S. leognanensis* Lambert, 1903), sub. desig., L. Agassiz, 1841; of *Lambertiella*, *L. pulchra* Checchia-Rispoli, monotypic.

(Figs. 3, c; 14, c; 18, a)

Large, thin, flattened scutellid echinoids; petals closed, length about half the radius of test; 4 genital pores; peristome small, central; periproct about midway between margin and peristome; margin of test with broad indentations corresponding to sutures between all columns, most prominent posteriorly; ambulaeral food grooves bifurcating just outside basicoronal plates;

basicoronal plates moderately large, ambulacrals and interambulacrals about equally developed; interambulacral columns all in contact with basicoronal plates, but narrower than adjacent ambulacrals at this point; ambulacral and interambulacral columns about equal at margin; oral post-basicoronal plates 6 or 7 to a column, very low near margin; periproct between first pair of post-basicoronal plates; pore-pairs conjugate, the outer elongate.

Upper Oligocene (?) to Miocene.

As here diagnosed, few if any of the species, other than the type, which have in the past been referred to *Scutella*, can be included within the genus. The position of the periproct is extremely advanced evolutionarily even though the post-basicoronal interambulacral plates are not separated from the basicoronal row. No New World species can be referred to *Scutella*. Many of the European Oligocene species may be referred to the genus *Parmulechinus* Lambert. Most of the European Miocene species which have been referred to *Scutella* appear to be congeneric with *S. leognanensis* Lambert, the type of *Parascutella* Durham (1953).

Checchia-Rispoli and subsequent authors have all considered his *Lambertiella* to be a laganid echinoid, presumably on the basis of the lack of ambulacral food grooves, although an examination of Checchia-Rispoli's illustrations shows this to be highly improbable. The margin of the test is thin and not inflated or rounded; the central petaloid area is considerably elevated above the margin; there are fairly well marked posterior marginal ambulacral indentations of the test as in most scutellids; the pattern of the plates on the apical surface is of a scutellid rather than a laganid or neolaganid type; finally, the interambulacra are relatively broader at the ambitus than in any of the laganids: for these reasons it would seem that *Lambertiella* must be a scutellid genus. The lack of ambulacral food grooves must be due to weathering, abrasion, or faulty preparation, or some similar cause. From its general aspect and the fact that the anterior petal is the longest, it appears probable that *Lambertiella* is a synonym of *Scutella*. Its type species is from the Miocene of Sicily.

Genus *Parascutella* Durham

Scutella auctores, in part, not Lamarek, 1816.

Parascutella Durham, 1953, Jour. Paleont., vol. 27, pp. 349-350.

Type species: *Scutella leognanensis* Lambert (1903) = *S. subrotunda* L. Agassiz (in part) (1841, pl. 17, figs. 1-11), not *Echinodiscus subrotundus* Leske, orig. desig.

(Fig. 18, b)

Large, thin, scutellid echinoids; petals moderately closed, length about two-thirds radius of test; a tendency for anterior petal to be shorter than posterior petals; pore-pairs conjugate; 4 genital pores; peristome moderately small, central; periproct submarginal, often with a groove to anal notch in margin of test; margin of test with broad indentations corresponding to all sutures, most prominent posteriorly; ambulacral food grooves of scutellid type, bifurcating just outside basicoronal plates; basicoronal plates moderately large, ambulacrals and interambulacrals about equally developed; interambulacral columns all just barely in contact with basicoronal interambulacral plates; 4 or 5 post basicoronal plates in each interambulacral column on oral surface; plates about half as high as wide near ambitus; periproct situated along suture between third pair of post-basicoronal plates; ambulacral and interambulacral areas of about equal width at margin.

Miocene, Europe.

The type species is from the Burdigalian of southern France. *Scutella neuvillei* Lambert is an Aquitanian species that is probably referable to this genus. *S. almerai* Lambert and *S. gibbercula* de Serres, from the Tortonian appear to be the youngest species belonging in the genus. It is somewhat uncertain whether forms like *S. truncata* Valenciennes of L. Agassiz (1841, pl. 16, figs. 1-10), *S. faujasii* de France (*ibid.*, pl. 15, figs. 4-6), and *S. propinqua* L. Agassiz (*ibid.*, pl. 16, figs. 11-16) should be considered in this genus or be assigned to a new genus. They are similar to *Parascutella* except that the periproct is farther from the margin and situated along the suture between the second and third post-basicoronal plates.

Genus *Parmulechinus* Lambert

Stenaster Lambert, 1905, Ann. Univ. Lyons, n.s., vol. 17, p. 140, not *Stenaster* Billings, 1858.

Parmulechinus Lambert, 1910, Rev. crit. Paléozool., vol. 10, p. 63; Durham, 1953, Jour. Paleont., vol. 27, pp. 349, 351.

Scutella auctores, in part.

Type species: *Parmulechinus labriei* (Lambert) = *Stenaster labriei* Lambert (1905) = *Scutella agassizi* Oppenheim (1902, pp. 68-69) (*fide* Lambert, 1915, pp. 19-29) = *S. striatula* L. Agassiz (1841, pl. 18, figs. 1-5), not *S. striatula* de Serres (1829), orig. desig.

(Fig. 18, *e*)

Medium-sized to large, scutellid echinoids; petals comparatively small, closed, length about one-half corresponding radius; 4 genital pores; peristome small, central; periproct submarginal to marginal; margin of test with broad indentations corresponding to all sutures, most prominent posteriorly; ambulacral food grooves bifurcating just outside basicoronal plates; basicoronal plates moderately large, similar to those of *Scutella*; interambulacra not as wide as ambulacra at ambitus.

Oligocene to Lower Miocene, Europe.

No undoubted specimens of the type species have been available. Specimens in the British Museum (Natural History) from the Tongrian of Malta, identified as *Scutella striatula* de Serres, have smaller petals and lack the distinct anal notch of the specimen figured as this species by L. Agassiz (1841, pl. 18, figs. 1-5). However, Oppenheim (1902, p. 68) made specific reference to Agassiz's illustrations when he proposed the name *S. agassizi* for the Oligocene species commonly called *S. striatula* de Serres, and therefore some other name should be used in referring to the Maltese species. The Maltese specimens resemble specimens of *S. subtetragona* de Grateloup (fig. 18, *e*) except that they seem to have an additional plate in each column of the ambulacra and interambulacra on the oral surface and the periproct is immediately submarginal.

If the Maltese specimens and *Scutella subtetragona* are congeneric with *S. agassizi*, an inference which seems to be supported by what appear to be narrow oral interambulacra in Lambert's (1915, pl. 4, fig. 2) illustrations of specimens transitional between his *Parmulechinus labriei* and adults of *S. agassizi*, then *Parmulechinus* is characterized by: a marginal or submarginal periproct between the fourth or fifth pair of post-basicoronal interambulacral plates; interambulacra about half the width of ambulacra at the ambitus; and petals about half the length of the corresponding radius.

In the general confusion surrounding the genus *Scutella*, this genus was thrown into its synonymy and forgotten as soon as Lambert (1915, pp. 19-29) recognized

that it was based on young specimens of *S. agassizi* Oppenheim. It appears possible that Lambert's figures (1915, pl. 4, figs. 1-6) may include the young of other species (especially figs. 5 and 6), as well as *S. agassizi*. Therefore, since Lambert apparently did not designate a type specimen for his *Stenaster labriei*, the specimen from which figures 1-3 of his 1915 paper were made is here designated the holotype.

According to Lambert (1915, p. 29), *S. agassizi* is a fairly widespread species, characteristic of the Stampian in southwestern France. The species is a member of a characteristic group of scutellid echinoids which, according to Cottreau (1913, p. 88), began in the lower Oliogocene and became extinct in the Burdigalian and includes *Scutella subtetragona* Grateloup (fig. 18, e), *S. lamberti* Airaghi, *S. peronai* Airaghi, *S. isseli* Airaghi, *S. melitensis* Airaghi, and *S. michaleti* Lambert.

Family Protoscutellidae n. fam.

Type genus: Protoscutella Stefanini.

Moderately large, flattened; petals moderately closed (fig. 1, l); outer member of pore-pair elongated; paired interambulaera barely in contact with basicoronal plates; posterior interambulacrum variable; interambulacral areas about as wide as ambulaera at ambitus; basicoronal interambulacral plates much larger than ambulacral plates (fig. 14, d); periproct on oral surface; ambulacral food grooves simple to bifurcating (fig. 3, e); genital pores 5.

Middle to upper Eocene, Gulf of Mexico, Atlantic Coast of North America.

The five genital pores seemingly make this a primitive family in accordance with its age, but the highly enlarged—and thus specialized—basicoronal interambulacral plates preclude it from the ancestry of most later scutellinid echinoids.

Genus *Protoscutella* Stefanini

Protoscutella Stefanini 1924, Bull. Geol. Soc. Amer., vol. 35, p. 843; Cooke 1942, Jour. Paleont., vol. 16, p. 17; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 390-391.

Type species: Scutella mississippiensis Twitchell, orig. desig.

(Fig. 32, f)

Medium-sized scutellid echinoids, test low, more or less rounded; lower surface usually slightly concave near margin; upper surface slightly domed in petaloid area; margins thin, rounded; usually a notch for periproct; petals slightly open, equal, length about half the radius of test; 5 genital pores; periproct submarginal, varying from close to margin to about one-fourth distance from margin; peristome central, small; ambulacral food grooves simple, unbranched; paired interambulacral areas on oral surface just touching basicoronal interambulacral plates; posterior interambulacrum separated from basicoronal plate by a pair of ambulacral plates meeting across interambulacral suture; interambulacral areas about two-thirds as wide as ambulacral areas at margin; interambulacral basicoronal plates quite large, half again as long as ambulacral basicoronal plates; ambulacral basicoronal plates small and narrow.

Middle to upper Eocene, southeastern and southern United States.

The type species is from the middle Eocene of the Gulf Coast. Cooke (1942, pp. 17-18) lists *Sismondia conradi* Cotteau, *Scutella tuomeyi* Twitchell, *Sismondia plana* Conrad, and *Protoscutella pentagonium* Cooke as other members of the genus.

Genus *Periarchus* Conrad

Periarchus Conrad, 1866, Smithson. Misc. Coll., vol. 7, no. 200, p. 21 (as subgenus of *Mortonia* Desor, not Gray); Stefanini, 1911, Boll. Soc. Geol. Ital., vol. 30, pp. 687-688; Lambert and

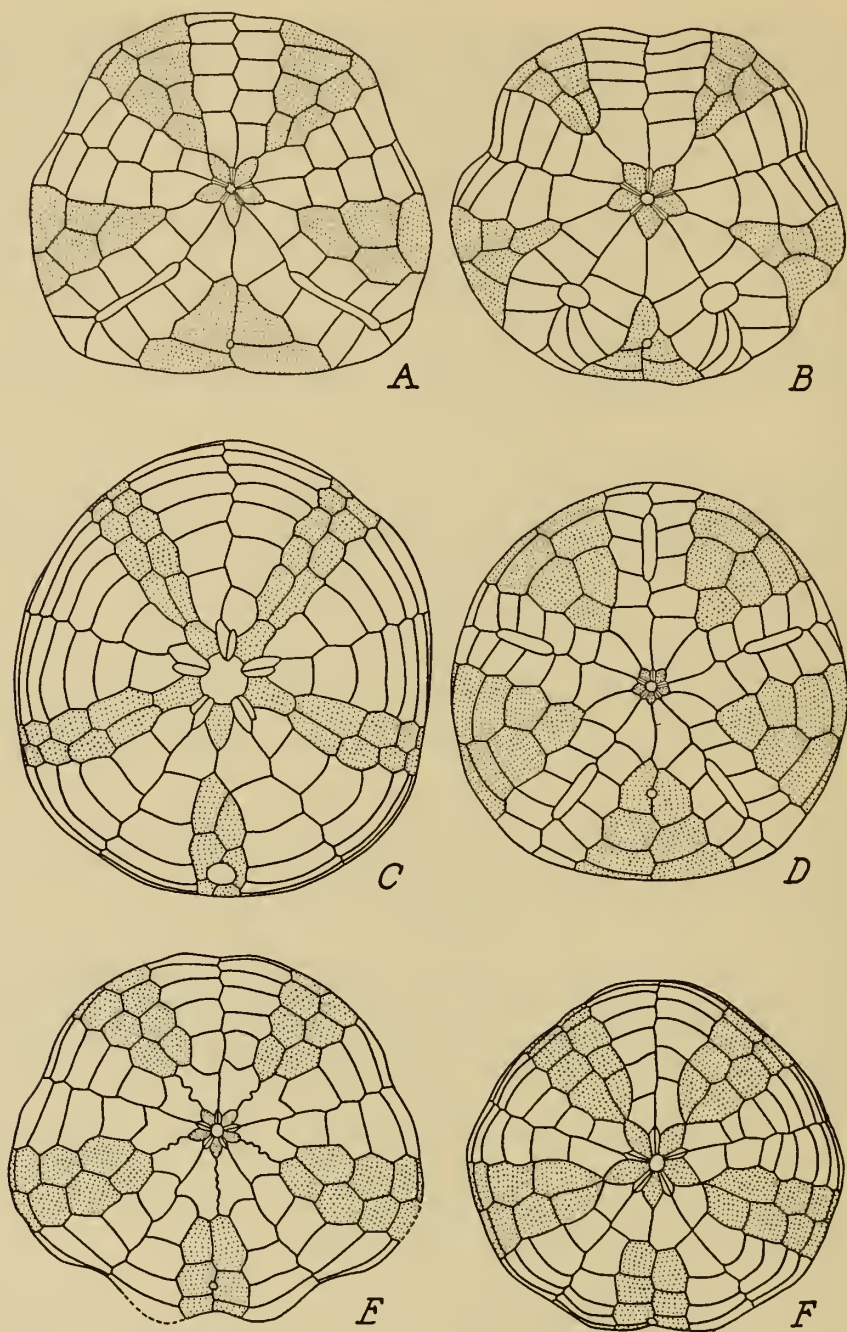


Fig. 32. Structure of oral surface of clypeasteroid echinoids: *a*, *Echinodiscus bisperforatus* Leske, $\times 0.57$, after L. Agassiz (1841, pl. 12, fig. 2). *b*, *Amphiope bioculata* (Des Moulins), $\times 0.9$, hypotype no. 33846; Miocene, Europe. *c*, *Pseudoastrodapsis nipponicus* (Nisiyama), $\times 2.4$; paratype no. 30131; "Mio-Pliocene," Japan. *d*, *Astriclypeus manni* Verrill, $\times 0.51$, hypotype no. 33390; Recent, Japan. *e*, *Abertella aberti* (Conrad), $\times 0.37$, hypotype, Johns Hopkins University Collections; Miocene, Maryland. *f*, *Protoscutella mississippiensis* (Twitchell), $\times 0.9$, hypotype no. 33821; upper Eocene, Mississippi.

Thiéry, 1914, Ess. nomencl. rais., p. 316; W. B. Clark and Twitchell, 1915, U. S. Geol. Surv. Mon. 54, p. 130; Cooke, 1942, Jour. Palcont., vol. 16, pp. 13-14; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 392-393.

Type species: Sismondia alta Conrad.

(Figs. 3, *e*; 14, *d*; 18, *d*)

Moderately large scutellid echinoids; margin of test moderately thin, flattened, petaloid area raised; oral surface flat; outline of test usually rounded, occasionally indented at sutures or with slight anal notch; petals open, slender, length slightly more than half radius of test, anterior petal slightly longer than others; 5 genital pores; periproct on oral surface, slightly more than midway from margin, small; peristome central, small; ambulacral food grooves bifurcating about midway from peristome; all interambulacral areas just touching interambulacral basicoronal plates, nearly as wide as ambulacral areas at margin, 4 or 5 post-basicoronal plates in each column on oral surface; usually 7 plates in ambulacral columns on oral surface; interambulacral plates of basicoronal row large, about twice as high as adjacent ambulacral plates; periproct along suture between first pair of post-basicoronal interambulacral plates.

Upper Eocene, southern and southeastern United States, Cuba.

The type and other species referred to this genus, as here restricted, are from the lower part of the "Late Eocene" as that term is used by Cooke. It is noteworthy that all typical species of this genus are from this interval and that *Scutella quinquefaria* Say and *Periarchus kewi* Cooke, both of which are referable to *Mortonella* Pomel, are from the "very Late Eocene," that is, *Mortonella* occurs in younger beds than *Periarchus*. Cooke (1942, pp. 13-14) synonymized the two genera, considering that the morphologic differences were of no more than specific rank. However, in the specimens at hand (fig. 18, *c* and *d*) representing the two genotypes, the periproct of *M. quinquefaria* has not advanced as far toward the basicoronal row as the periproct of *P. lyelli* var. *pileus-sinensis*, indicating that the genotype of *Periarchus* had evolved farther in this direction than that of *Mortonella*. This difference is slight, it is true; but when considered with the fact that the species of *Mortonella* are of slightly younger geologic age and are much less flattened it seems significant. The petals of *M. quinquefaria* and *M. kewi* are also somewhat more inflated than those of *Periarchus*. It seems that these differences warrant considering the two as separate genera.

Genus *Mortonella* Pomel

Mortonia Desor, 1858, Synop. des échin. foss., p. 231, not *Mortonia* Gray 1851.

Mortonella Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 70; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 316; Stefanini, 1911, Boll. Soc. Geol. Ital., vol. 30, pp. 684-685; W. B. Clark and Twitchell, 1915, U. S. Geol. Surv. Mon. 54, p. 128; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 391-392; Durham, 1952, Bull. Zool. Nomencl., vol. 6, pp. 168-169.

Type species: Scutella rogersi Morton as figured by L. Agassiz (1841, pl. 19*a*, figs. 1-4), not *S. rogersi* Morton (1834), monotypic.

(Fig. 1, *l*; 18, *c*)

Large scutellid echinoids; margins of test thick, rounded, petaloid area raised or not, oral surface flat; outline of test rounded or with slight indentations; petals open, somewhat broader than in *Periarchus*, length about five-eighths radius of test, anterior petal slightly longer than others; 5 genital pores; periproct on oral surface about midway from margin; peristome central, small; ambulacral food grooves bifurcating about midway from peristome; all interambulacral areas barely in contact with basicoronal plates, about as wide as ambulacral areas at

ambitus; usually 4 post-basicoronal plates in each interambulacral column on oral surface; usually 7 post-basicoronal plates in each ambulacral column on oral surface; basicoronal interambulacral plates much larger than basicoronal ambulacral plates, about twice as high; periproct at junction of sutures between first and second pair of post-basicoronal interambulacral plates.

As here restricted, the genus includes the type and *M. kewi* (Cooke) from the upper part of the "Late Eocene" of the Atlantic and Gulf Coast as that term is used by Cooke (1942). *Scutella cubae* and *S. camagüeyana* Weisbord (1934) from the upper Eocene of Cuba appear to belong in this genus, according to the illustrations, although Weisbord compared them to *S. tuomeyi* Twitchell, which is referred to *Protoscutella*.

For differentiation of this genus from *Periarchus* Conrad, see the discussion under that genus.

According to a strict interpretation of Article 30 of the International Rules of Zoological Nomenclature, and Opinions 65 and 168, the type of *Mortonella* should be *Scutella rogersi* Morton, not L. Agassiz (1841), a species which is currently referred to the genus *Clypeaster*. However, *Mortonella* has consistently been used for the scutellid echinoid figured by L. Agassiz ever since the proposal of the name. Accordingly, it is being used in that sense here while a petition (Durham, 1952b) asking that the name be validated in the accepted sense is presented to the International Commission on Zoological Nomenclature.

Family Eoscutellidae n. fam.

Type genus: Eoscutella Grant and Hertlein.

Moderately large, flattened, thin, laterally elongated, with well-developed internal supports; petals well developed, moderately closed; a few isolated primary pore-pairs outside end of petals; outer member of pore-pair elongated; interambulacra continuous on oral surface, about half as wide as ambulacra at ambitus; basicoronal interambulacral plates much larger than ambulacral plates; 4 genital pores; periproct marginal; ambulacral food grooves bifurcating just outside basicoronal plates.

Middle and upper Eocene, California and Oregon.

Genus *Eoscutella* Grant and Hertlein

Eoscutella Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, p. 54;

Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 386.

Type species: Scutella coosensis Kew, orig. desig.

(Figs. 3, *f*; 16, *f*; 18, *f*)

Test more or less ovate in outline, elongated laterally, thin; oral surface flat, aboral surface slightly arched, margins very thin; margin of test evenly rounded or with broad indentations in anterior ambulacral areas, and at times a well-developed, broad anal notch; petals partly closed, length about half the anterior radius of the test; genital pores 4; periproct small, marginal; peristome central, small; ambulacral food grooves bifurcating fairly close to peristome and extending to margin; on oral surface interambulacral areas are narrow and continuous; basicoronal interambulacral plates very large, almost occluded from contact with peristome; basicoronal ambulacral plates very small, about one-third the length of the basicoronal interambulacral plates; internal supports highly developed.

Middle and upper Eocene, California and Oregon.

The Coaledo formation of Oregon in which the type species occurs is of about

lower upper Eocene age. The type species is not known elsewhere, but there are in the University of California collections two incomplete echinoids (U.C.M.P. hypotypes nos. 15989, 15990) of similar aspect from beds of middle Eocene age near Martinez, California. Unfortunately, the incompleteness of the specimens prevents positive conclusions, but one specimen (no. 15989) has a notch for the periproct and appears to have been only moderately elongated laterally. The other (no. 15990) was much more elongated laterally than *Scutella coosensis*—apparently it was somewhat more than twice as wide as long. They do not appear to represent the same species, but both—particularly no. 15990—appear to be referable to *Eoscutella*. The marginal notch for the periproct in no. 15989 might preclude its assignment to this genus.

In the Stanford University collections there is a specimen referable to this genus, and apparently representing another new species, from the Eocene (Matilija sandstone?) of Echo Falls, Santa Paula Canyon, Ventura County, California. The upper surface is eroded, there is a wide notch for the periproct, and the specimen is about twice as wide as long.

Grant and Hertlein suggested a comparison of this genus with *Periarchus* Conrad and *Echinarachnius* Gray. The branching ambulacral furrows easily distinguish it from the latter; and the four genital pores, differently branching ambulacral furrows, and marginal periproct readily distinguish it from *Periarchus*.

Mortensen indicates that *Scutella vaquerosensis* Kew may also be "reasonably" referred to *Eoscutella*; but this species has straight, unbranched ambulacral furrows, and very differently arranged plates on the oral surface. It does not appear to be closely related to the type species of *Eoscutella*.

Although this is the earliest recorded scutellinid echinoid, the bifurcating ambulacral furrows, very large basicoronal interambulacral plates, and highly developed internal supports indicate that it is already highly specialized and is not the ancestor of later members of the suborder.

Family Dendrasteridae Lambert, emended

Dendrasteridae Lambert, 1899, Bull. Soc. Sci. Yonne, vol. 53, pt. 2, table opp. p. 50; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 316 (in part).

Phelsumasteridae Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 316 (in part).

Scutellidae Gray, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 344–359 (in part).

Medium-sized to large, flattened, usually well-developed internal supports; petals well formed (fig. 1, *d*), a few isolated pores outside petals; paired petals more or less closed, anterior petal more widely open; outer member of pore-pair elongated; interambulacrum 5 discontinuous on oral surface; interambulacra nearly as wide as ambulacra at ambitus; basicoronal interambulacral plates larger than ambulacral plates; 4 genital pores; periproct inframarginal to supramarginal; ambulacral food grooves bifurcating (fig. 4, *e*) or trifurcating just outside basicoronal plates.

Pliocene to Recent, Pacific Coast of North America and Japan.

The genus *Dendraster* appears in characteristic form in the basal beds of the Pacific Coast Pliocene. According to current correlations, two separate lineages, represented by *D. gibbsii* Rémond and *D. elsmerensis* Durham (1949), appear at about the same time at the base of the Pliocene. *D. elsmerensis* has a marginal periproct and thus is primitive in this respect, but the thin margin is a specialized

character. It would appear that there must be an as yet unrecognized upper Miocene species ancestral to these two. *Scutellaster*, with its supramarginal periproct and paired interambulacra not disconnected on the oral surface, is more primitive than *Dendraster* but is known only from the upper Pliocene. It is difficult to explain the relationship of the Japanese *Scaphechinus* to the three western American genera, but all available criteria seem to indicate that it belongs in this group.

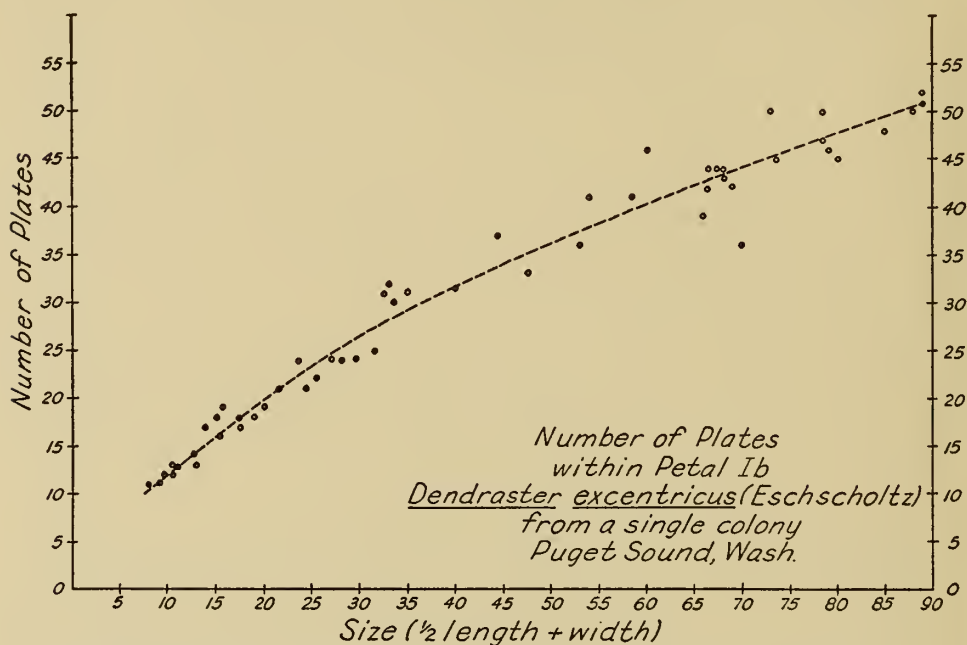


Fig. 33. Number of plates within petal Ib of *Dendraster excentricus* (Eschscholtz).

Genus *Dendraster* L. Agassiz

Dendraster L. Agassiz, L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 135; Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 16; Desor, 1858, Synop. des échin. foss., p. 234; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 70; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 319; Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, pp. 78-79; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 380-381; Durham, 1949, Amer. Jour. Sci., vol. 247, pp. 50, 58.

Echinarachnius Gray, A. Agassiz, 1872-1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, pp. 107, 315, 524 (in part); Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 158-159 (in part).

Type species: *Dendraster excentricus* L. Agassiz = *Scutella excentrica* Eschscholtz = *Echinarachnius excentricus* Valenciennes, monotypic.

(Figs. 1, d; 4, c; 5, b; 11; 20; 21, a-d; 26, j; 33)

Medium-sized to large, flattened; apical system often posteriorly excentric, raised; margins of test moderately thin; paired petals moderately closed, anterior petal elongated, more open than paired petals; a few isolated primary pores outside petals; periproct inframarginal, close to margin, between second and third pair of post-basicecoronal plates; peristome central; ambulacral food grooves complexly developed, usually extending onto aboral surface, usually most strongly developed posteriorly; basicecoronal plates relatively small, interambulacral plates about twice as

large as ambulacral plates; interambulacra all discontinuous on oral surface, separated by a pair of ambulacral plates; 3 or 4 post-basicoronal interambulacral plates to column on oral surface; posteriorly 5 or 6 and anteriorly 7 or 8 pairs of post-basicoronal ambulacral plates on oral surface.

Lower Pliocene to Recent, Gulf of California to Puget Sound.

Dendraster laevis H. L. Clark (fig. 21, *d*) is a Recent species from depths of 4 to 30 fathoms that has little or no excentricity of the apical system. A few fossil species are similar. It has been suggested informally that *laevis* should be referred to some other genus; but in all characters other than excentricity it is a typical *Dendraster*.

Argamakova (1934) has reported Pacific Coast species of *Dendraster* (*Calaster*), along with *Astrodapsis* and *Echinarachnius* from Sakhalin. As indicated elsewhere (Durham, 1952a), some of the identifications are certainly incorrect. The species referred to *Dendraster* (*Calaster*), if correctly identified, should be referred to *Scutellaster* [*Anorthoscutum*].

Mansfield (in Mertie, 1931, p. 130) has reported *Dendraster gibbsii* from upper Miocene or Pliocene rocks of Lituya Bay, Alaska. Mansfield's original material was not available for examination, but specimens from the same area, although superficially similar to *D. gibbsii*, represent a new species of *Echinarachnius*.

Dendraster excentricus often lives in extensive colonies, sometimes with several hundred individuals per square yard. In areas where they are not too strongly affected by wave action or other disturbances, they stand on edge, or slightly inclined, with the anterior one-third or less of the test buried in the sand and the rest of the test extending up into the water. It seems that the excentricity of the apical system and greater posterior development of the food grooves is correlated with this habit. The nonexcentric species probably lie flat on the sea floor.

Genus *Scutellaster* Cragin

Scutellaster Cragin, 1895, Amer. Geol., vol. 15, pp. 90-91; W. B. Clark and Twitchell, 1915, U. S. Geol. Surv. Mon. 54, p. 67; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 321; Reeside, 1924, Proc. U. S. Nat. Mus., vol. 66, art. 20, pp. 1-4; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 397; Durham, 1953, Jour. Paleont., vol. 27, pp. 147-149.

Anorthoscutum Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 319; Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, pp. 91-92; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 393; Durham, 1949, Amer. Jour. Sci., vol. 247, pp. 52, 61.

Calaster Kew, 1920, Univ. Calif. Publ. Geol. Sci., vol. 12, p. 130.

Type species: of *Scutellaster*, *S. cretaceus* Cragin = *Scutella interlineata* Stimpson = *Anorthoscutum interlineatum* (Stimpson) = *Dendraster* (*Calaster*) *interlineatus* (Stimpson), monotypic; of *Anorthoscutum*, *A. interlineatum* Stimpson, orig. desig.; of *Calaster*, *Scutella interlineata* Stimpson, subs. desig., Grant and Hertlein, 1938.

(Figs. 4, *d*; 34, *f*; 35, *a* and *b*; pl. 1, figs. 1, 2, 5, 7, 8; pl. 2, fig. 5)

Medium-sized to large, flattened; margin of test thin to moderately thick; apical system slightly posteriorly excentric; apical system sometimes raised, highest point anterior to center of system; outline of test varying from rounded to broadly indented at interambulacral areas; anterior petal open, others more or less closed; petals slender to moderately inflated, length about three-fourths radius of test; poriferous areas of anterior petal narrower than in paired petals; periproct supramarginal, between second pair of plates from ambitus; peristome central; ambulacral food grooves trifurcating about one-third distance from peristome, poorly developed an-

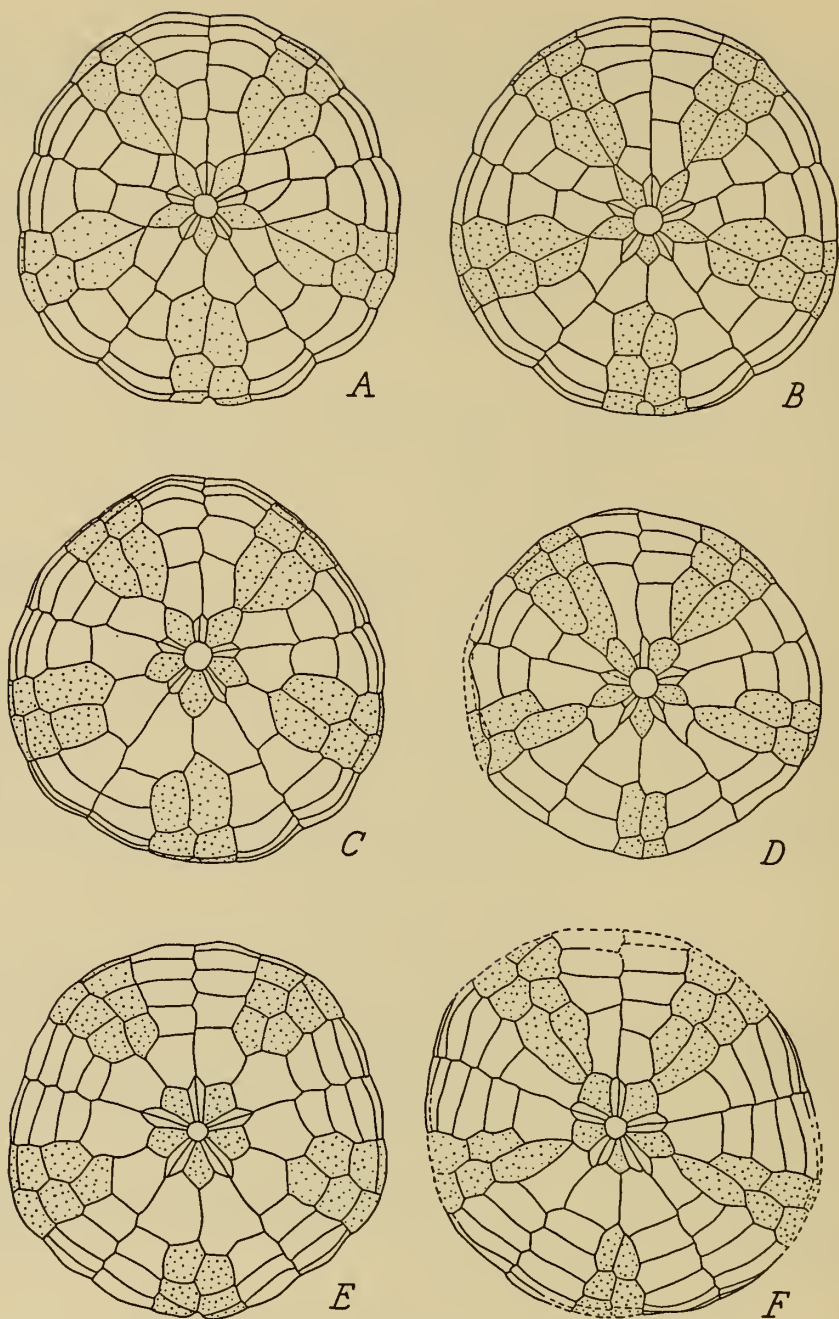


Fig. 34. Structure of oral surface of clypeasteroid echinoids: *a*, *Echinarachnius parma* (Lamarek), $\times 1.0$, oral view (note aberrant suture in IVb), hypotype no. 33827; Recent, New England Coast. *b*, *E. parma* (Lamarek), $\times 1.14$, oral view of another individual from same locality as fig. 1, hypotype no. 33828. *c*, *E. parma* (Lamarek), $\times 1.0$, oral view (same specimen as text fig. 2, *b*, Durham, 1949, but better prepared), hypotype no. 32931; Recent, Kodiak Island, Alaska; interambulacrum 5 reverse of normal. *d*, *Kewia blancoensis* (Kew), $\times 2.85$, oral view of unfigured paratype no. 30132; middle Miocene, Oregon. *e*, *Scaphechinus mirabilis* forma *japonica* (von Martens), $\times 0.72$, oral view, hypotype no. 33359; Recent, Tokyo Bay. *f*, *Scutellaster interlineatus* (Stimpson), $\times 0.68$, oral view, hypotype no. 32870; upper Pliocene, California.

teriorly; basicoronal plates moderately large, interambulacral plates as large as or larger than ambulacral plates; both columns of anterior interambulacra in contact with basicoronal plates; posterior column only of posterior paired interambulacra in contact with basicoronal plates; 2 or 3 post-basicoronal interambulacral plates to column on oral surface; 4 or 5 post-basicoronal ambulacral plates to column on oral surface; interambulacral columns about half as wide as ambulacral columns at ambitus.

Middle and upper Pliocene, central California to Oregon, Sakhalin (?).

Argamakova (1934, pp. 36, 41, pl. 1, fig. 5) has recorded *Scutellaster*, as *Dendraster* (*Calaster*) *oregonensis*, from Sakhalin. His illustrations and description are such that the identification cannot be verified. It is doubtful whether his material is correctly referred to this genus.

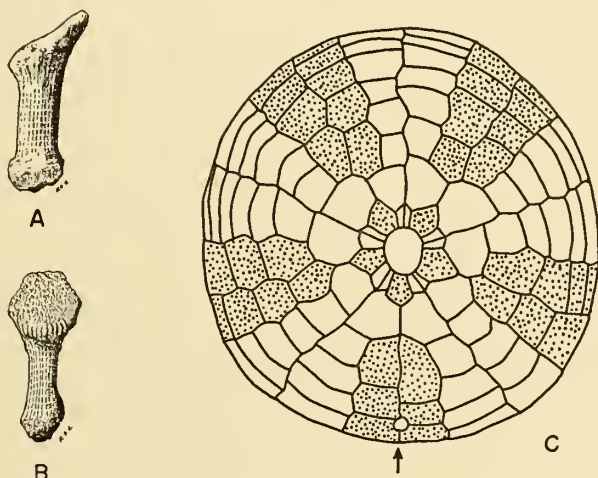


Fig. 35. *Scutellaster* and *Merriamaster*. *a* and *b*, primary spines from aboral surface of *Scutellaster interlineatus* (Stimpson), hypotype no. 33857, $\times 27.5$; Pliocene, California; drawings by R. S. Creely. *c*, *Merriamaster perrini* (Weaver), hypotype no. 32948, $\times 2.1$; Pliocene, California.

It has been shown elsewhere (Durham, 1953c) that the type specimen of *Scutellaster* Cragin (1895) is a badly worn specimen of the common *Scutella interlineata* Stimpson; thus *Scutellaster* has priority over *Anorthuscutum*.

The poor development of the anterior ambulacral food grooves seems to indicate that, like *Dendraster*, some members of this genus assumed an inclined position on the ocean floor. Recently, a fossil locality containing individuals that retain their spines has been found. On the aboral surface, the spines are short and club-shaped (fig. 35), with the head expanding abruptly to a broad crown, producing a distinct pavement similar to that occurring in *Encope wetmorei* A. H. Clark. The aboral miliary spines are long and slender. On the oral surface, the primary spines are long and slender like those of *Dendraster*.

Genus *Merriamaster* Lambert

Merriamaster Lambert, 1911, Rev. crit. Paléozool., vol. 15, p. 64; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 312; Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, pp. 64–65; Stewart, 1941, U. S. Geol. Surv. Prof. Pap. 195, pp. 81–82; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 396–397; Durham, 1949, Amer. Jour. Sci., vol. 247, pp. 55, 58–59.

Orchoporus Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 293; Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, pp. 50–51; Stewart, 1941, U. S. Geol. Surv. Prof. Pap. 195, p. 82; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 236.

† *Twitchellia* Lambert 1916, Rev. crit. Paléozool., vol. 20, p. 171; Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, pp. 50–51 (under *Orchoporus*).

Type species: of *Merriamaster*, *Scutella perrini* Weaver, orig. desig.; of *Orchoporus*, *O. koehleri* Lambert and Thiéry, monotypic. According to Stewart (1941, p. 82), *O. koehleri* is apparently a young specimen of *Scutella perrini* Weaver. This conclusion is substantiated by the available growth series of the latter species. Type species of *Twitchellia*, by original designation: *Astrodapsis merriami* Anderson of W. B. Clark and Twitchell (in part) = *Orchoporus lamberti* Grant and Hertlein (1938), not *A. merriami* Anderson.

(Figs. 4, *f*; 35, *c*)

Medium-sized, moderately flattened, with rounded margins; outline of test rounded to rostrate posteriorly; apical system slightly excentric posteriorly, anterior petal longest; petals extending about three-fourths distance to margin, usually open, but sometimes slightly closed; periproct usually just submarginal, often on slight rostrum; peristome central, ambulacral food grooves in adult bifurcating about one-third distance from peristome, extending onto aboral surface in large individuals; basicoronal plates of moderate size, interambulacra larger than ambulacra; post-basicoronal interambulacral plates not in contact with basicoronal plates in adults; usually 3 or 4 post-basicoronal interambulacral plates to column on oral surface; 5 to 7 post-basicoronal ambulacral plates to column on oral surface; internal radial supports simple, moderately developed; internal concentric supports only slightly developed.

Upper Pliocene, central and southern California.

The lack of abundant concentric internal supports, the greater number of plates on the oral surface, the more open character of the petals, the rounded margin, and the differently developed ambulacral food grooves separate *Merriamaster* from *Dendraster*. It may be distinguished from *Astrodapsis* by the bifurcating food grooves of the adults and the excentric position of the apical system.

In young individuals of *M. perrini* the food grooves appear simple; in medium-sized individuals they seem to have only a simple bifurcation, but in large adults they can be seen to extend onto the aboral surface. The presence of a rostrum for the periproct seems to vary individually, but in some specimens it is very prominent.

The illustration of the type of *Twitchellia* strongly suggests that it is a specimen of one of the upper Pliocene species which has somehow been mislabeled as from the middle Miocene.

Genus *Scaphechinus* A. Agassiz

Scaphechinus A. Agassiz, 1863, Proc. Acad. Nat. Sci. Philadelphia, vol. 15, p. 359; Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, p. 56, n.; Nisiyama, 1940, Jubilee Publ. Commem. Prof. H. Yabe, pp. 832–835; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 374.

Chaetodiscus Lütken, 1864, Vidensk. Medd. naturh. Foren. Kjøbenhavn for 1863, p. 172.

Scutella Lamarek, Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 317 (in part). Not Lamarek.

Echinarachnius Gray, A. Agassiz, 1872–1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, pp. 107, 524 (in part), not Gray.

Echinarachnius Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 158–159 (in part), not Leske.

Type species: of *Scaphechinus*, *S. mirabilis* A. Agassiz, monotypic; of *Chaetodiscus*, *C. scutella* Lütken = *S. mirabilis* A. Agassiz, monotypic.

(Figs. 4, *e*; 5, *a*; 6, *d*; 26, *k*; 34, *e*)

Medium-sized to large, flattened, outline subrounded to subpentagonal, margin often indented at sutures; apical system central; petals well formed, slightly open, length about two-thirds radius; petaloid region slightly depressed, with interambulacral depressions extending to ambitus; periproct marginal; peristome central; ambulacral food grooves bifurcating just outside basicoronal plates; basicoronal plates large, interambulacral plates much larger than ambulacral; interambulacral areas all separated from basicoronal row by a pair of ambulacral plates; 3 or 4 post-basicoronal interambulacral plates to column on oral surface; 4 or 5 post-basicoronal ambulacral plates to column on oral surface; internal concentric and radial supports well developed; interambulacra nearly as wide as ambulacra at ambitus.

Pliocene to Recent, Japan, Formosa.

The discontinuous interambulacral areas on the oral surface and fewer oral plates readily differentiate *Scaphechinus* from *Scutella*. The depressed apical area, much larger basicoronal plates, and marginal periproct separate it from *Dendraster*. The depressed apical area, bifurcating food grooves, and fully discontinuous interambulacra differentiate it from *Echinarachnius*.

Family Echinarachniidae Lambert, emended

Echinarachniidae Lambert, Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 314 (in part).

Phelsumasteridae Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 316 (in part).

Scutellidae Gray, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 344-359 (in part).

Medium-sized to large, more or less flattened; internal supports usually well developed; petals (fig. 1, *i*) well formed, usually open, a few isolated pores outside petals, outer member of pore-pair slightly elongated, usually not subdivided; interambulacrum 5 usually discontinuous in advanced species; width of interambulacra at ambitus variable but usually two-thirds (or less) width of ambulacra; basicoronal interambulacral plates larger than ambulacral plates; 4 genital pores; periproct marginal to inframarginal; ambulacral food grooves (fig. 3, *b*) with central trunk, sometimes with lateral branches near ambitus.

Lower Miocene to Recent, Pacific Coast of North America to Japan; Recent, northeastern coast of North America.

The more widely open petals and ambulacral food grooves with a central trunk indicate that this family is less specialized than the Dendrasteridae.

Genus *Echinarachnius* Gray⁴

Echinarachnius Gray, 1825, Ann. Philos., n.s., vol. 10, p. 428 (in part); L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, p. 88; Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, pp. 14-15; Desor, 1858, Synop. des échin. foss., p. 230 (in part); A. Agassiz, 1872-1873, Mem. Mus. Comp. Zool. Harvard Coll., vol. 3, pp. 107, 524 (in part); Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 158-159 (in part); H. L. Clark, 1911, Ann. Mag. Nat. Hist., ser. 8, vol. 7, pp. 598, 605 (in part); Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, pp. 56-57 (in part); Nisiyama, 1940, Jubilee Publ. Commem. Prof. H. Yabe, pp. 804-819 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 363-367; Durham, 1949, Amer. Jour. Sci., vol. 247, pp. 52-62 (in part). Not *Echinarachnius* Leske, 1778, nor Lambert and Thiéry, 1914.

Phelsumia Pomel, 1883, Class. method. et gén. échin. viv. et foss., p. 70, new name for *Echinarachnius* Gray, not Leske. Not *Phelsuma* Gray, 1840.

Phelsumaster Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 316, new name for *Phelsumia* Pomel, not *Phelsuma* Gray.

Type species of *Echinarachnius*: *Scutella parva* Lamarek, subs. desig., L. Agassiz, 1841.

⁴ Placed on Official List of Generic Names by action of International Congress of Zoology, Paris, 1948. See Bull. Zool. Nomencl., vol. 4, p. 535, 1950.

(Figs. 1, *i*; 3, *b*; 6, *e*; 8, *a*; 9, *a*; 10, *a*; 23; 24; 26, *l*; 34, *a-c*; pl. 2, fig. 4)

Medium-sized, flattened; outline rounded, more or less indented at sutures; upper surface gently arched, oral surface flat; petals about three-fifths length of radius, widely open, flaring at end; poriferous zones narrow, outer pore not subdivided; peristome of moderate size, central; periproct marginal, between third pair of post-basicoronal plates; ambulacral food grooves straight, trifurcating about one-third distance from margin, extending to ambitus; basicoronal plates rather large, interambulacral plates about twice as high as ambulacral plates; basicoronal interambulacral plates somewhat variable in relation to post-basicoronal plates, just barely in contact in all areas in some specimens, in others in contact only in areas 2 and 3; usually 3 post-basicoronal plates in each interambulacral column on oral surface except in 2*b* and 3*a*, which have 4 plates; usually 5 post-basicoronal ambulacral plates in each column on oral surface except in II*b* and III*a*, which may have 6; interambulacral areas about two-thirds as wide as ambulacral areas at ambitus.

Miocene to Recent, northwestern Pacific areas; Pliocene to Recent, northeastern Pacific; and Recent, northwestern Atlantic.

The type species, especially specimens from the northeastern shores of the United States, is very variable (figs. 23 and 24). Individual specimens from the same locality vary from quite flattened to quite inflated; the madreporite may be small or large; the basicoronal plates vary considerably in relative size and in their relationship to the post-basicoronal plates in the interambulacral areas (table 2). Normally the anterior petal is longer than the posterior petals but not consistently so.

The discontinuous distribution of *E. parma*, occurring on the Pacific Coast from Puget Sound to the Aleutian Islands and Japan, and on the Atlantic Coast from Labrador to Maryland, without any intervening records in the Arctic region, is unique. Mortensen (1948, p. 373) has concluded that the species migrated through the Arctic region in some epoch warmer than the present one. Because of the apparent lack of differentiation of the populations in the two areas, it seems improbable that this could have occurred earlier than the Pliocene.

Echinarachnius appears to have been dominantly a northwestern Pacific genus during the Tertiary. None of the Pacific Coast species referred to it by Grant and Hertlein (1938) are to be referred to it, and of those listed by Nisiyama (1940), only *E. microthyroides* Nisiyama, *E. laganolithinus* Nisiyama, *E. parma obesa* H. L. Clark, *E. parma sakhalinenis* Argamakowa, and *E. asiaticus* Michelin are to be included in the genus. *Echinarachnius subtumidus* Nisiyama and Hashimoto (1950), from the Miocene of Hokkaido, is another representative. An undescribed species occurs in probable Pliocene of Lituya Bay, Alaska.

Genus *Kewia* Nisiyama

Kewia Nisiyama, 1934, Jour. Geol. Soc. Japan, vol. 41, no. 489, p. 362 (genus without species); 1935, Saito Ho-on Kai Mus. Research Bull. 5, p. 136, n.; 1940, Jubilee Publ. Commem. Prof. H. Yabe, pp. 819-821 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 366-367.
Type species: *Scutella blancoensis* Kew, orig. desig.

(Figs. 3, *a*; 34, *d*; 36, *f*)

Small to medium-sized scutellid echinoids; oral surface flat, aboral surface moderately arched, highest point usually slightly anterior to apical system; outline rounded, at times slightly elongated posteriorly; anterior petal open, paired petals moderately closed; petals about two-

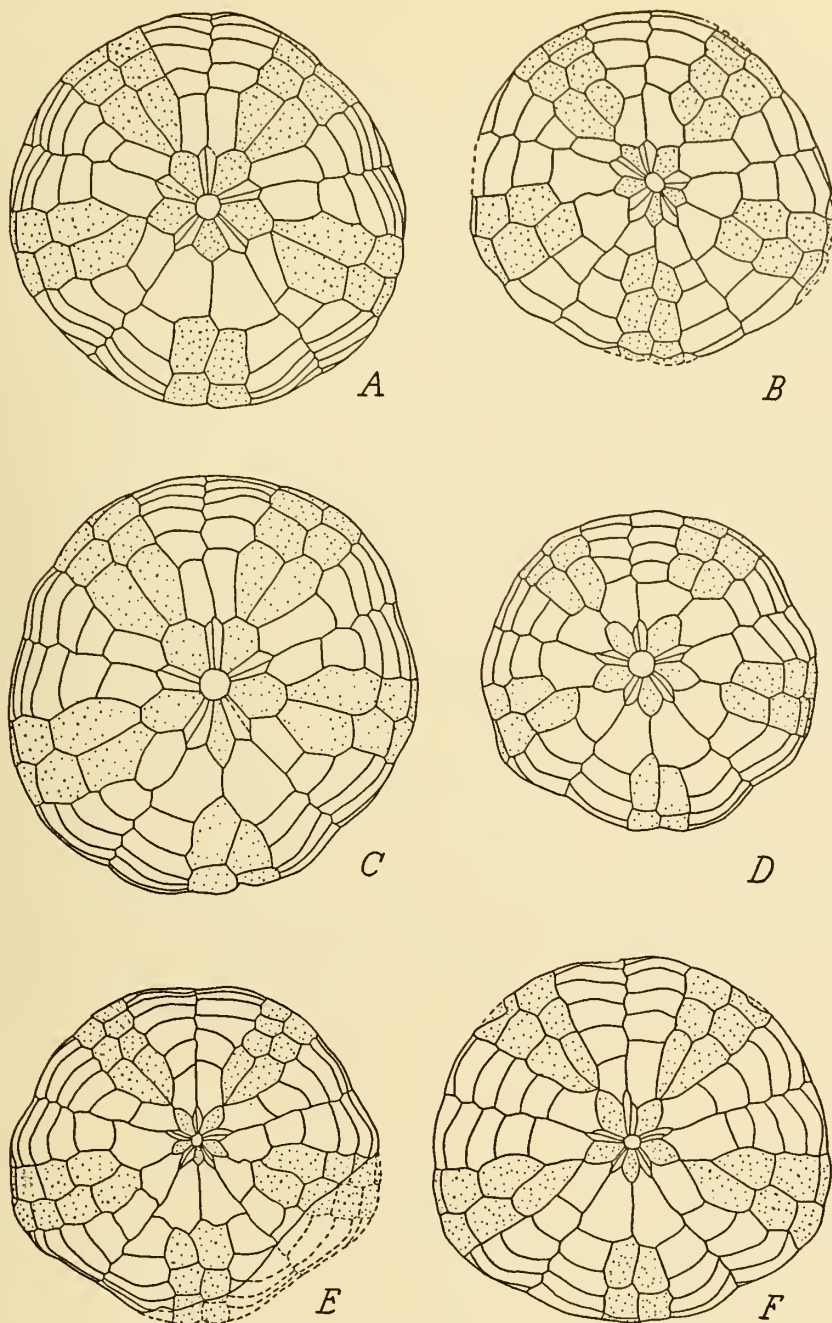


Fig. 36. Structure of oral surface of clypeasteroid echinoids: *a*, *Remondella gabbii* (Rémond), $\times 1.8$, oral view of typical individual, hypotype no. 33401; upper Miocene, California. *b*, *Tenuirachnius kleinpelli* (Grant and Hertlein), $\times 1.5$, oral view, hypotype no. 11370; upper Miocene, California; arrow indicates axis of slight lateral crushing. *c*, *Remondella gabbii* (Rémond), $\times 2$, oral view of nontypical individual, hypotype no. 11368 (figured by Kew, 1920, pl. 12, figs. 4, *a* and *b*); upper Miocene, California. *d*, *Vaquerosella merriami* (Anderson), $\times 2$, oral view, hypotype no. 33441; middle Miocene, California. *e*, *Vaquerosella vaquerosensis* (Kew), $\times 0.5$, oral view (partly restored), "cotype" no. 11403 (figured by Kew, 1920, pl. 9, fig. 1, *c*); lower Miocene, California. *f*, *Kewia fairbanksi* (Arnold), $\times 0.9$, oral view, hypotype no. 11360 (figured by Kew, 1920, pl. 11, fig. 2, *c*); lower Miocene, California.

thirds length of radius; pore-pairs conjugate; peristome central, moderately large; periproct supramarginal, close to margin; ambulacral food grooves simple, unbranched; basicoronal plates of moderate size, somewhat irregular in type species, interambulacral plates considerably larger than ambulacral plates; post-basicoronal plates in interambulacra 1, 2, 3, and 4 in contact with basicoronal plates or approximately so; area 5 widely separated from basicoronal row; on oral surface interambulacral areas 1a, 2a, 2b, 3a, 3b, and 4b with 3 post-basicoronal plates, areas 1b, 4a, 5a, and 5b with 2 or 3 post-basicoronal plates to a column; post-basicoronal ambulacral plates on oral surface 3 to 5 to a column; interambulacral areas one-third to one-half as wide as ambulacral areas at ambitus, with area 5 narrowest.

Oligocene to Miocene, Pacific Coast of North America and Japan.

Kew and Nisiyama both considered *Scutella blancoensis* to be of Oligocene age; Schenck (1928, p. 42) concluded that the beds from which the type came are probably of Pliocene age, but it has been shown (Durlam, 1953a) that *S. blancoensis* is from beds of middle Miocene age. Weaver (1943, pp. 5-6) has recorded it from the Montesano formation of Washington of upper Miocene or lower Pliocene age, and the "variety" *etheringtoni* Weaver from the Astoria formation of middle Miocene age. *Echinarachnius* (*Kewia*) *parvus* Nisiyama and *E. (Kewia) elongatus* Nisiyama from the Oligocene and Miocene of Japan were referred to this genus by Nisiyama. He also indicated that *Scutella nipponica* Nagao may be a member.

Scutella newcombi Kew from the Sooke formation of Vancouver Island was described and figured as having its periproct on the oral surface. The type specimen has a very small opening at the point indicated by Kew, but it also has another, with fractured margins, just supramarginal in position (see Kew, 1920, pl. 8, fig. 2, a). An unfigured paratype has a supramarginal periproct and no opening at the point indicated by Kew. Thus this species should be referred to *Kewia*. *Scutella fairbanksi* Arnold and possibly *S. fairbanksi santanensis* Kew from the California lower Miocene seem to be referable to this genus.

It appears possible that *Kewia* represents the ancestral stock from which *Scutellaster* as well as many of the Pacific Coast echinarachniids are derived.

Kewia may be differentiated from *Echinarachnius* by its supramarginal periproct, more elongate first pair of post-basicoronal interambulacral plates, and by the greater closure of the paired petals.

Genus *Vaquerosella* n. gen.

Type species: Scutella andersoni Twitchell.

Small to large, flattened; margin of test more or less strongly indented at posterior ambulacra, less distinctly at other ambulacra; apical system slightly anterior, petals more or less raised; anterior petal wide open, paired petals slightly closed; petals two-thirds to three-fourths length of radius; outer member of pore-pair moderately elongate; periproct marginal; peristome very slightly anterior; ambulacral food grooves simple, unbranched, at times indistinct; basicoronal plates well developed; basicoronal interambulacral plates wider but not always higher than interambulacral plates; post-basicoronal interambulacral plates usually separated from basicoronal plates; 3 or 4 post-basicoronal interambulacral plates to column in paired interambulacra on oral surface; 2 post-basicoronal plates to a column in posterior interambulacrum on oral surface; 5 or 6 post-basicoronal plates to column in 3 anterior ambulacra on oral surface, sometimes only 4 plates in two posterior ambulacral columns; interambulacra about two-thirds width of ambulacra at ambitus.

Lower Miocene, California, Baja California.

(Fig. 16, *c*; 21, *e* and *f*; 36, *d* and *e*)

In addition to the type species, *Scutella norrisi* Pack (in part—holotype and similar specimens; not Kew, 1920, pl. 10, fig. 1, *a*, nor Loel and Corey, 1932, Univ. Calif. Publ. Bull. Dept. Geol. Sci., vol. 22, pl. 6, fig. 2), *S. tejonensis* Kew, and probably *S. vaquerosensis* Kew are referable to this genus. *S. vaquerosensis* (fig. 36, *e*) is more extended laterally, consistently has one or two more plates to a column in the oral ambulaeal and interambulaeal areas, and has somewhat larger basicoronal interambulaeal plates, and thus differs from the type species and *S. norrisi* Pack. Two species appear to have been confused under *S. norrisi* by Kew and by Loel and Corey. Some of the specimens (Kew, 1920, pl. 10, fig. 1, *a*, not 1, *b*; Loel and Corey, 1932, Univ. Calif. Publ. Bull. Dept. Geol. Sci., vol. 22, pl. 6, fig. 2) referred to this species have the petals more widely open and nearly flush, and a width of test greater than the length. Pack's holotype (fig. 21, *f*) has rather strongly raised petals, the petals less widely open, and a length about equal to the width. The species confused with *S. norrisi* by Kew and by Loel and Corey is here renamed *Vaquerosella coreyi*, with the original of Loel and Corey's figure 2 as holotype (U.C.M.P. no. 31712) and Kew's specimen (U.C.M.P. no. 11027) as paratype. *V. coreyi* is apparently similar to *S. vaquerosensis* in its plate arrangement. *Astrodapsis merriami* Anderson (fig. 36, *d*) may also be referable to this genus.

The well-marked posterior ambulaeal notching of the test and tendency to a width greater than length are characteristic.

Genus *Astrodapsis* Conrad

Astrodapsis Conrad, 1856, Proc. Acad. Nat. Sci. Phila., vol. 8, p. 315; W. B. Clark and Twitchell, 1915, U. S. Geol. Surv. Mon. 54, p. 197; Kew, 1920, Univ. Calif. Publ. Geol., vol. 12, pp. 78–80; Lambert and Thiéry, 1925, Ess. nomencl. rais., p. 582 (correction of spelling on p. 314); Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, pp. 68–69; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 393–395; Nisiyama, 1948, Jour. Paleont., vol. 22, pp. 601–602 (in part); Durham, 1952, Jour. Paleont., vol. 26, pp. 844–846.

Asterodaspis Conrad, A. Agassiz, 1872, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, p. 172.

Arachnoides Breynius, Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 165 (in part).

Astrodaspis Conrad, Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 314.

Type species: Astrodapsis antiselli Conrad (not Kew, 1920 = *A. salinasensis* Richards), monotypic.

(Fig. 3, *d*; 14, *f*; 22, *a–f*)

Medium-sized to large, outline rounded to elongate to pentagonal, margin thin to inflated; margin indented, slightly to moderately at posterior paired ambulaeal, less strongly at others; petals very slightly to very strongly raised, madreporite correspondingly slightly to strongly depressed; petals broad, open, anterior petal more widely open than lateral petals; petals extending two-thirds to three-fourths distance to margin; aboral surface with more or less strongly developed broad interambulaeal grooves extending from apical system to margin; periproct marginal to just submarginal on species with inflated margins; ambulaeal food grooves with central axis extending to margin, about one-third distance from margin a pair of lateral branches, all three may extend onto aboral surface nearly to apical system; peristome central; basicoronal plates variable in development, but interambulaeal plates more strongly developed than ambulaeal plates; primitive species with paired interambulaeal just in contact with basicoronal plates, advanced species with interambulaeal discontinuous on oral surface; 4 or 5 post-basicoronal interambulaeal plates to column on oral surface; 5 (in primitive species) to 9 (in

advanced species) post-basiconal ambulaeal plates on oral surface; marginal ambulaeal plates on oral surface often with very low altitude; interambulaeal nearly as wide as ambulaeal at ambitus; periproct between third or fourth pair of post-basiconal plates.

Middle Miocene to lower Pliocene, California.

As noted elsewhere (Durham, 1952a), it appears highly improbable that any of the species of this genus reported from Sakhalin or Kamchatka are correctly identified. *Astrodapsis nipponica* Nisiyama has been made the type of *Pseudoastrodapsis* Durham (1953b) = *Nipponaster* Durham (1952a), not *Niponaster* Lambert. *Pseudoastrodapsis* is characterized by very narrow and continuous paired interambulaeal on the oral surface, as contrasted with the relatively wide and usually discontinuous interambulaeal areas of *Astrodapsis*.

Astrodapsis brewerianus (Rémond) (fig. 22, f) is a primitive species which is apparently ancestral to the more specialized members of the genus. Its continuous paired interambulaeal and marginal periproct indicate that it cannot be derived from any of the species currently referred to either *Vaquerosella* or *Kewia*, but it appears probable that the three must have a common ancestor. It seems possible that several subgeneric taxa might ultimately be differentiated within the genus as now constituted: the species with slightly raised petals and rounded ambitus; the large, flattened species with thin margin and barely raised petals; and the typical group with raised petals and moderately thick margins. However, the relationships of the various species need to be studied more carefully before this is attempted.

Astrodapsis gregersoni Grant and Eaton (fig. 22, e) is gerontic in several respects: its extremely raised petals, the irregularly but excessively developed basiconal interambulaeal plates, and so forth.

Genus *Pseudoastrodapsis* Durham

Nipponaster Durham, 1952, Jour. Paleont., vol. 26, pp. 844–846. Not *Niponaster* Lambert, 1920.

Pseudoastrodapsis Durham, 1953, Jour. Paleont., vol. 27, p. 756.

Type species: *Astrodapsis nipponicus* Nisiyama, orig. desig.

(Figs. 16, e; 32, c)

Small to medium-sized, more or less inflated; oral surface moderately flattened, aboral surface arched; margin rounded, outline slightly elongate; petals wide open, about equally so, length about three-fourths radius, slightly elevated; apical system slightly anterior; periproct submarginal; peristome central; ambulaeal food grooves simple; basiconal plates moderately developed, interambulaeal plates considerably higher than ambulaeal plates; paired interambulaeal continuous on oral surface, posterior interambulaeum separated from basiconal plates, periproct between second and third pair of post-basiconal plates; interambulaeal areas about one-fourth width of ambulaeal at ambitus; paired interambulaeal with 4 or 5 post-basiconal plates to column on oral surface; ambulaeal with 6 or 7 post-basiconal plates to column on oral surface.

"Mio-Pliocene" of Japan.

It seems highly probable that the species of *Astrodapsis* recorded from Sakhalin and Kamchatka (see Durham, 1952a) are to be referred to this or some closely allied genus.

Genus *Remondella* n. gen.

Type species: *Clypeaster gabbii* Rémond.

(Figs. 14, *e*; 36, *a*, *c*)

Medium-sized, oral surface flattened, aboral surface arched, ambitus moderately acute, outline irregularly rounded; apical system slightly anterior, petals not raised; anterior petal wide open, paired petals slightly closed; petals about two-thirds length of radius; periproct marginal; peristome central; ambulacral food grooves simple, indistinct; basicoronal plates well developed, interambulacral plates considerably larger than ambulacral; paired interambulacra in contact with basicoronal plates, with 3 or 4 post-basicoronal plates on oral surface; posterior interambulacrum discontinuous with 2 post-basicoronal plates on oral surface; ambulacra with 5 or 6 post-basicoronal plates on oral surface, outer 3 or 4 plates with very low altitude.

Upper Miocene to lower Pliocene, California.

The continuous paired interambulacra, marginal periproct, and peripheral oral ambulacral plates with relatively low altitude distinguish this genus from *Kewia*. *Vaquerosella* usually has discontinuous paired interambulacra and a more flattened test. It appears that several species were probably confused under the type species by Kew. *Scutella gabbi* var. *tenuis* Kew is here made the type species of *Tenuirachnius*, n. gen. It does not appear to be very closely related to *Clypeaster gabbii* Rémond.

Genus *Tenuirachnius* n. gen.

Type species: Scutella gabbi var. *tenuis* Kew = *Echinarachnius gabbii kleinpelli* Grant and Hertlein. Not *E. tenuis* Yoshiwara.

(Fig. 36, *b*)

Medium-sized, thin, flattened, outline irregularly rounded, more or less strongly indented at posterior ambulacra; margin thin; petals about two-thirds length of radius, not raised, anterior petal wide open, paired petals slightly closed; apical system slightly anterior; periproct very slightly supramarginal; peristome central; ambulacral food grooves simple, indistinct; basicoronal plates well developed, interambulacral plates larger than ambulacral plates; interambulacral areas apparently all discontinuous on oral surface, anterior pair almost in contact with basicoronal plates; 3 or 4 post-basicoronal interambulacral plates to column on oral surface; 4 or 5 post-basicoronal ambulacral plates to column on oral surface; altitude of peripheral ambulacral plates on oral surface moderate.

Upper Miocene, California.

The thin, flattened test, three pairs of post-basicoronal oral interambulacral plates in area 5, and marginal ambulacral plates without greatly reduced altitude are characteristic.

Family Monophorasteridae Lahille

Monophorinae Lahille, 1896, Rev. Mus. La Plata, vol. 7, pp. 441-442 (in part); Stefanini, 1911, Boll. Soc. Geol. Ital., vol. 30, p. 749; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 324 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 419 (in part).

Scutulinae Lambert, Stefanini, 1911, Boll. Soc. Geol. Ital., vol. 30, p. 749 (in part).

Phelsumasteridae Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 316 (in part).

Scutellinae Lahille, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 360 (in part).

Medium-sized, flattened, with well-developed internal supports; well-defined but variably open petals; outer member of pore-pair elongated; pores conjugate; interambulacra continuous, narrower at ambitus (fig. 29, *e* and *f*) than midway on oral surface; basicoronal interambulacral plates much larger than ambulacral plates; periproct on oral surface; ambulacral food grooves bifurcating (fig. 2, *d*) just outside basicoronal plates; 4 genital pores.

Miocene, Patagonia, Chile.

Because of the presence of a single small posterior lunule in *Monophoraster* it has been considered ancestral to *Encope*, *Mellita*, and *Leodia* and all have been placed in the same subfamily. However, the large basicoronal interambulacral plates and the continuous paired interambulacra that narrow (sometimes extremely) toward the ambitus indicate that the South American genera are not closely related to the group mentioned above, for they have relatively small and undifferentiated basicoronal plates and orally discontinuous paired interambulacra that widen toward the ambitus. In addition, there are primitive but characteristic species of *Encope* in the "lower Miocene" of the Caribbean area.

The only specimen of *Iheringiella patagoniensis* Desor examined (fig. 29, *f*) seems to be an extremely conservative variant of the species as figured by Lahille (1898, pls. 1 and 2). His figures (1898, figs. 1, 2, 10; 1896, figs. 28, 29, 30, 36) show that *Iheringiella* is much more closely related to *Monophoraster* than the specimen figured here would indicate. Lahille (1898, p. 450) has concluded that *Iheringiella* is the immediate ancestor of *Monophoraster*. His illustrations show a great deal of variation in the narrowness of the interambulacra at the ambitus.

Genus *Monophoraster* Lambert and Thiéry

Monophora Desor, 1847, Bull. Soc. Géol. France, ser. 2, vol. 4, p. 287; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss, p. 70; Lahille, 1896, Rev. Mus. La Plata, vol. 7, pp. 411-444. Not *Monophora* Bory de St. Vincent, 1804, or Quoy and Gaimard, 1824.

Monophoraster Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 324; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 419-420.

Type species: *Monophora darwini* Desor, monotypic.

(Fig. 29, *e*)

Moderately large, flattened, scutellid echinoids with a posterior anal lunule; petals fairly large, partly closed, length nearly two-thirds radius of test, anterior petal longest, peristome moderately large, central; periproct moderately small, midway on oral surface, with shallow groove leading to small lunule immediately posterior to it; margin of test with broad indentations corresponding to ambulacral areas, two posterior indentations deepest; ambulacral food grooves branching in a manner similar to *Encope*; basicoronal interambulacral plates very large, ambulacral basicoronal plates relatively very small; interambulacral areas greatly constricted as they approach ambitus on both oral and aboral surfaces; about four post-basicoronal plates on oral surface in each interambulacral column, about five post-basicoronal plates on oral surface in ambulacral columns; periproct and lunule between first pair of post-basicoronal plates.

The type species is from the Miocene of Argentina. Two other species, *M. duboisi* Cotteau from Parana and *M. caldensis* Gigoux from Chile, are recorded.

The generic diagnosis given above is based on Lahille's (1896) detailed description and figures and on examination of two specimens (Harvard Univ. Mus. Comp. Zoöl. no. 3371 and U.C.M.P. hypotype no. 33358) from Patagonia. *Monophoraster* does not appear to be closely related to any other genus except *Iheringiella*, which also has narrow interambulacral areas but is not nearly so specialized in its development. By restriction of the interambulacral areas at the ambitus, further enlargement of the basicoronal interambulacral plates, migration of the periproct toward the peristome, and development of a lunule, *Monophoraster* can be derived from *Iheringiella*.

Genus *Iheringiella* Berg

Iheringia Lahille, 1898, Rev. Mus. La Plata, vol. 8, p. 437, not Keyserling, 1891.

Iheringiella Berg, 1898, Comun. Mus. Nac. Buenos Aires, vol. 1, fasc. 1, p. 16 (new name for *Iheringia* Lahille).

Iheringiana Berg, 1898, Comun. Mus. Nac. Buenos Aires, vol. 1, fasc. 1, p. 41 (new name for *Iheringiella* Berg, not *Iheringella* Pilsbry, 1893); Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 319; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 388-390.

Iheringina Lahille, 1899, Rec. Mus. La Plata, vol. 9, p. 395 (new name for *Iheringia* Lahille).

Type species: *Scutella patagoniensis* Desor, monotypic.

(Figs. 2, *d*; 29, *f*)

Medium-sized, scutellid echinoids; oral side flat, aboral surface slightly arched; petals partially closed to open and lyrate, length about two-thirds radius of test; margin of test smooth or broadly indented; peristome central, of moderate size; periproct submarginal; ambulacral food grooves, simple, bifurcating about one-fourth distance from peristome; basicoronal plates with interambulacra much larger than ambulacra; interambulacral areas much narrower than ambulacral areas on both oral and aboral surfaces, and usually very narrow at ambitus; interambulacral areas with 3 or 4 post-basicoronal plates in each column on oral surface, ambulacral areas with 4 or 5 plates per column on oral surface; first pair of post-basicoronal interambulacral plates considerably elongated; periproct situated at junction of sutures between second and third pair of post-basicoronal plates.

The above diagnosis is after the description and figures of Lahille (1898) and a specimen (hypotype no. 76032) in the Princeton University Department of Geology collections. It is to be noted that the figures of Ortmann (1902) are highly stylized and obviously not true to the original specimens. The type species is from the lower Miocene of Argentina. Lahille considered that there were five different morphologic varieties of the species. From the distribution notes and by comparison with similar cases in other scutellinid echinoids it is to be suspected that some or all of his varieties may be of specific rank.

This genus does not appear to be closely related to any other scutellinid except *Monophoraster*.

As the rules of nomenclature are now understood, *Iheringiella* is not a homonym of *Iheringella*; consequently this form of the generic name should be used, not *Iheringiana*.

Family Mellitidae Stefanini

Monophorinae Lahille, 1896, Rev. Mus. La Plata, vol. 7, p. 441 (in part); Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 324 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 419 (in part).

Mellitinae Stefanini, 1911, Boll. Soc. Geol. Ital., vol. 30, p. 749.

Medium-sized to large, flattened; well-developed internal supports; posterior interambulacral and paired ambulacral lunules or indentations; petals well defined, moderately closed (fig. 1, *k*); pores conjugate, outer member of pore-pair elongated, a few primary pore-pairs outside petals; paired interambulacra not in contact with basicoronal plates on oral surface; interambulacra on oral surface widening toward ambitus, about as wide as ambulacra at ambitus; basicoronal plates (fig. 16, *b*) fairly small, interambulacral plates slightly larger than ambulacral plates; periproct on oral surface between posterior interambulacral lunule and peristome; ambulacral food grooves bifurcating just outside basicoronal plates.

Lower Miocene to Recent, tropical and warm temperate coasts of the Americas.

Genus *Mellita* L. Agassiz

Mellita L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, p. 34 (in part); L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 138 (in part); Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 22 (in part); Desor, 1858, Synop. des échin. foss., pp. 236-237 (in part); A. Agassiz, 1872-1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, pp. 140, 319, 534 (in part); Pomel 1883, Class. méthod. et gén. échin. viv. et foss., p. 71 (in part); Duncan, 1889 Jour. Linn. Soc. London, Zool., vol. 23, pp. 161-162 (in part); Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 324; H. L. Clark, 1940, Proc. U. S. Nat. Mus., vol. 89, p. 436; Mortensen, 1948, Mon. Echin. vol. 4, pt. 2, pp. 420-422; Durham, 1952, Bull. Zool. Nomencl., vol. 6, pp. 359-360. Not *Mellita* Fabricius, 1823 (see Durham, 1952).

Type species: Echinodiscus quinquesperforatus Leske = *Mellita testudinata* Klein (pre-Linnean), subs. desig., Pomel, 1883.

(Figs. 16, *b*; 17, *a*; pl. 2, fig. 1)

Medium-sized to large, thin, flattened; margin thin, outline rounded to subpentagonal; maximum height of test anterior to apical system; paired ambulacral and posterior interambulacral lunules; lunules narrow and elongate, normally closed in adult; apical system slightly anterior; petals well defined, moderately closed, anterior petal slightly more open than others; anterior odd and posterior paired petals about equal in length, anterior paired petals shorter; outer member of pore-pair greatly elongated, not subdivided; peristome distinctly anterior, ambulacral food grooves bifurcating just outside basicoronal plates; posterior interambulacral lunule extending nearly to peristome on oral surface; periproct just within anterior part of posterior lunule on oral surface; basicoronal plates small; paired interambulacra not in contact with basicoronal row, separated by a pair of ambulacral plates, with 3 post-basicoronal plates per column on oral surface; posterior interambulacrum in contact with basicoronal plates, periproct partly within basicoronal interambulacral plate; first post-basicoronal plates of posterior interambulacrum extending half length of lunule; ambulacra with 4 to 6 post-basicoronal plates per column on oral surface; 4 genital pores.

Miocene to Recent, tropical and warm temperate shores of the Americas.

The first pair of post-basicoronal interambulacral plates in the paired areas tends to be elongated, in contrast to the first pair in *Leodia*, which is short.

Genus *Leodia* Gray

Leodia Gray, 1852, Proc. Zool. Soc. London 1851, pt. 19, p. 36; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 324; H. L. Clark, 1940, Proc. U. S. Nat. Mus., vol. 89, p. 435; Cooke, 1942, Jour. Paleont., vol. 16, p. 22; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 421-422, 429. *Mellita auctores*, in part.

Type species: Leodia richardsonii Gray = *Echinodiscus sexiesperforatus* Leske = *Echinus hexaporus* Gmelin = *Scutella sexforis* Lamarck, monotypic.

(Figs. 1, *k*; 7, *i*; 17, *b*)

Rather large, thin, flattened; margin of test thin; maximum height of test at apical system; 5 ambulacral lunules and a posterior interambulacral lunule; lunules elongate, narrow; posterior lunule almost entirely outside line connecting distal end of posterior petals; apical system slightly posterior; 4 genital pores; petals well developed, small, nearly closed, approximately equal in length; outer member of pore-pair greatly elongated, not subdivided; peristome central, small; periproct just outside basicoronal plates, shallow groove from periproct to anterior end of lunule; ambulacral food grooves bifurcating just outside basicoronal plates; basicoronal plates small; paired interambulacra separated from basicoronal plates by 2 pairs of ambulacral plates; 2 or 3 post-basicoronal interambulacral plates to column in paired areas on oral surface; posterior interambulacrum in contact with basicoronal plates, 4 post-basicoronal plates to column; 4 or 5 post-basicoronal ambulacral plates to column on oral surface.

Pleistocene to Recent, eastern coast of Americas from the Carolinas to Río de la Plata.

Mortensen (1948, pp. 432-433, pl. 60, figs. 6 and 7) has referred *Mellita pacifica* Verrill to this genus on the basis of a single specimen from Ecuador, supposedly representing Verrill's species, in the Copenhagen Museum. His illustration shows a specimen which he states has only four genital pores (this cannot be verified from the figure) and which lacks the elongate posterior petals of *Encope*, but which has lunules more like those of *Encope* and a periproct not in contact with the basicoronal plates. If this specimen is referable to *Leodia*, then the diagnosis given above should be modified in regard to the position of the periproct and shape of the lunules. However, it does not look like a *Leodia* as here recognized.

Genus *Mellitella* Duncan

Mellitella Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 162; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 325; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 448-449; Durham, 1950, Geol. Soc. Amer. Mem. 43, pt. 2, p. 49 n.

Type species: Encope stokesii Agassiz, monotypic.

(Figs. 17, *e* and *f*; 27, *f*; pl. 1, fig. 3)

Medium-sized, flattened; margin of test thick or thin; greatest height at apical system; 5 small marginal, ovate ambulacral lunules, partly closed to open; a posterior interambulacral closed lunule, outside line connecting distal end of posterior petals; apical system posterior; petals well formed, slightly open, anterior petal more open than paired petals; posterior paired petals shortest, anterior petal longest; outer member of pore-pair greatly elongated, not subdivided; 5 genital pores; peristome small, slightly posterior; ambulacral food grooves bifurcating at margin of basicoronal plates; basicoronal plates small; all interambulacral areas separated from basicoronal plates by pair of ambulacral plates; periproct approximately at inner end of first post-basicoronal plates; interambulacra usually with 3, rarely 2, post-basicoronal plates to column on oral surface; ambulacra with 4 or 5 post-basicoronal plates to column on oral surface; periproct midway between peristome and posterior lunule, with shallow groove to lunule.

Miocene to Recent, Pacific Coast of Americas, Miocene of Caribbean areas.

M. stokesii is represented in the Museum of Paleontology of the University of California collections by more than forty Recent specimens from Ecuador. At least one, and perhaps two, undescribed living species from the Gulf of California-Central American region are indicated by fragmentary material characterized by lunules much larger than those of the type species. *Encope angelensis* and *E. scrippsae* (Durham, 1950) from the Pliocene of the Gulf of California should be referred to this genus. Two undescribed fossil species from the Miocene of Venezuela are also abundantly represented in the Museum of Paleontology collections. The Venezuelan species have a thicker margin than the Pacific Coast species.

The group of echinoids referred to this genus are characterized by the slightly posterior apical system, by the long anterior petal, and by the interambulacral lunule posterior to a line connecting the distal ends of the posterior petals. Mortensen and others have discussed the internal structure and suggested that it is intermediate between *Mellita* and *Encope*. However, the arrangement of the plates on the oral surface indicates that in this respect it is more advanced than either of those genera. Both *Mellita* and *Encope* have the plates of the posterior interambulacral area in contact with the basicoronal interambulacral plate, but in *Mellitella* this area is disjunct, being separated from the basicoronal row by the

first post-basicoronal plates of the adjacent ambulacral areas. Also, the periproct is situated at the inner edge of the disjunct interambulacral area, instead of being at the margin of the basicoronal plates. In addition, the first post-basicoronal plates of each column of the anterior interambulacral areas are more elongate and narrower than in *Encope*.

Genus *Encope* L. Agassiz

Echinodiscus Leske, 1778, Add. ad Klein, p. 195 (in part).

Encope L. Agassiz, 1840, Cat. syst. ectyp. échin., pp. 6, 17; 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, p. 45 (in part); L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 137 (in part); Desor, 1858, Synop. des échin. foss., p. 237 (in part); A. Agassiz, 1872-1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, pp. 126, 324, 544 (in part); Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 71 (in part); Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 160; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 325; A. H. Clark, 1946, Smithson. Misc. Coll., vol. 106, no. 5, pp. 2-9; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 433-436; H. L. Clark, 1948, Univ. So. Calif. Publ., Allan Hancock Pac. Exped., vol. 8, pp. 319-324; Durham, 1950, Mem. Geol. Soc. Amer., no. 43, pt. 2, pp. 42-43.

Moulinia L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, pp. 3, 139; A. Agassiz, 1872, Mem. Mus. Comp. Zoöl. Harvard College, vol. 3, pp. 326-328.

Moulinia L. Agassiz, L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, p. 139 (pro *Moulinia* L. Agassiz).

Echinoglyphus van Phelsum, Gray, 1852, Proc. Zool. Soc. London 1851, pt. 19, p. 37; not *Echinoglycus* van Phelsum, L. Agassiz, 1841; Leske, 1778 (in part).

Echinoglycus van Phelsum, Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 24. Not *Echinoglycus* van Phelsum, L. Agassiz, 1841.

Ravenellia Lütken, 1864, Vidensk. Medd. naturh. Foren. Kjøbenhavn for 1863, p. 168. Not *Ravenellia* McCrady, 1859.

Macrophora Conrad, 1865, Proc. Acad. Nat. Sci. Phila., ser. 2, vol. 9, p. 134.

Desmoulinaster Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 294 (pro *Moulinia* L. Agassiz 1847, not Grateloup, 1841).

Type species: of *Encope*, *E. grandis* L. Agassiz, monotypic; of *Moulinia*, *M. cassidulina* L. Agassiz = *Scutella cassidulina* Des Moulins = young of *Encope emarginata* (Leske), *vide* A. Agassiz (1872, pp. 326-328), monotypic; of *Ravenellia*, *Scutella macrophora* Ravenel, monotypic; of *Macrophora*, *Scutella macrophora* Ravenel, by tautonymy. H. L. Clark's (1911) designation of *Echinodiscus emarginatus* Leske as the type of *Encope* [*Eucope* by misprint] L. Agassiz, 1841 is invalid because the genus was first proposed in 1840 with *grandis* as the only species listed.

(Figs. 4, *b*; 9, *h*; 12, *f*; 16, *a*; 17, *c* and *d*)

Medium-sized to large, flattened; margin of test thick or thin; greatest height variable in position; 5 ambulacral open notches or variably closed lunules; a posterior closed interambulacral lunule, more than half of lunule anterior to line connecting distal end of paired posterior petals; lunules variable in shape; apical system somewhat anterior, 5 genital pores; petals well formed, nearly closed, anterior petal usually slightly more open than paired petals; posterior paired petals longest, anterior paired petals shortest; outer member of pore-pair greatly elongated, sometimes subdivided deep within test; peristome slightly anterior; ambulacral food grooves bifurcating at edge of basicoronal plates; basicoronal plates small, posterior interambulacral plate largest; paired interambulacra separated from basicoronal plates by first pair of post-basicoronal ambulacral plates; posterior interambulacrum either in contact with or slightly separated from basicoronal plate; interambulacra with 3 or 4 post-basicoronal plates to column on oral surface; ambulacra with 5 or 6 post-basicoronal plates to column on oral surface; periproct at inner margin of first pair of post-basicoronal plates, situated at anterior end of slope or groove leading into posterior lunule.

Lower Miocene to Recent, warm temperate and tropical shores of Americas.

Numerous fossil and Recent species have been described. The longer posterior petals and the anterior apical system easily differentiate *Encope* from *Mellitella*.

Echinoglycus [*Echinoglyphus* Gray, 1852] van Phelsum is apparently a Latin rendition by Leske of van Phelsum's "Egelkoek" (Phelsum, 1774, pp. 26, 34-35), which first appears in the synonymy of *Echinodiscus bisperforatus* Leske (1778, p. 197) in the combination (referring to van Phelsum's work) "onregelmatige Egelkoek, *Echinoglycus irregularis*," and subsequently appears, in combination with various specific names, in the synonymy of most of the species referred to *Echinodiscus* by Leske. *Echinoglycus* as such does not appear in van Phelsum's work and should be credited to Leske. L. Agassiz (1841, pp. 2, 3), considered *Echinoglycus* to be precisely equivalent to his genus *Mellita*. Gray (1852, p. 37; 1855, p. 24) used *Echinoglycus* (spelled *Echinoglyphus* in 1852) for *Encope* of L. Agassiz. So far as can be determined, no type has ever been designated for *Echinoglycus*; therefore, in order to dispose of the name, *Echinoglycus irregularis* Leske [pro onregelmatige Egelkoek, van Phelsum], an absolute synonym of *Echinodiscus bisperforatus* Leske, is here designated as the type species. It is thus a junior absolute synonym of *Echinodiscus* Leske, the type (*E. bisperforatus*) of which was fixed by action of the International Commission on Zoological Nomenclature (see Bull. Zool. Nomencl., vol. 4, p. 535, 1950).

Family Astriclypeidae Stefanini

Astriclypeinae Stefanini, 1911, Boll. Soc. Geol. Ital., vol. 30, pp. 747, 748, 749 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 398.

Rotulinae Gray, Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 321 (in part). Not Gray, 1855.

Medium-sized to large, flattened; well-developed internal supports; with paired posterior ambulaeral lunules or notches, anterior ambulaeral lunules may be present; petals (fig. 1, *m*) well defined, occasionally a primary pore-pair outside petal; outer member of pore-pair elongated; posterior interambulaera discontinuous on oral surface, anterior interambulaera may be discontinuous; interambulaera about as wide as ambulaera at ambitus; basicoronal interambulaeral plates (fig. 16, *d*) much larger than ambulaeral plates; 4 genital pores; periproct on oral surface; ambulaeral food grooves (fig. 4, *a*) bifurcating just outside basicoronal row.

Miocene of Europe, Miocene to Recent, Indo-Pacific to Japan.

Genus *Astriclypeus* Verrill

Astriclypeus Verrill, 1867, Trans. Conn. Acad. Arts Sci., vol. 1, p. 311; A. Agassiz, 1872-1873, Mem. Mus. Comp. Zool. Harvard Coll., vol. 3, pp. 93, 538; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 71; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 163; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 323; Nisiyama, 1935, Res. Bull. Saito Ho-on Kai Mus., no. 5, pp. 132-145; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 414-416; Morishita, 1952, Mem. Coll. Sci., Univ. Kyoto, ser. B, vol. 20, pp. 107-114.

Crustulum Troschel, 1868, Niederrh. Gesel. f. Natur und Heilkunde, p. 1.

Type species: of *Astriclypeus*, *A. manni* Verrill, monotypic; of *Crustulum*, *C. gratulans* Troschel = *A. manni* Verrill, monotypic.

(Figs. 1, *m*; 32, *d*)

Large, flattened, with 5 ambulaeral lunules; aboral surface raised, margin thin; apical system central, petals well defined, nearly closed; outer member of pore-pair not subdivided; peristome central; basicoronal plates small; interambulaeral areas separated from basicoronal plates by first pair of post-basicoronal ambulaeral plates; interambulaera with 3 or 4 post-basicoronal plates to column on oral surface, with areas widening toward ambitus so that they are slightly wider than ambulaeral areas at ambitus; ambulaeral areas with 6 or 7 post-basicoronal plates to

column on oral surface; first post-basicoronal ambulaeral plates with about twice altitude of subsequent plates; periproct about midway between peristome and ambitus, between first pair of post-basicoronal interambulaeral plates; broad groove from inner end of lunules to basicoronal plates.

Lower Miocene to Recent, Cambodia to southern Japan.

Nisiyama (1935, fig. 2) has illustrated a specimen from the "Burdigalian" of Formosa with the three anterior lunules very slightly developed and the posterior lunules well developed. He believes that this indicates that *Astriclypeus* is derived from an *Echinodiscus*-like ancestor. *Astriclypeus manni* subsp. *ambigenus* Nisiyama (lower Miocene, Japan) has ovate instead of narrow elongate lunules.

Genus *Echinodiscus* Leske

Echinodiscus Leske, 1778, Add. ad Klein, pp. 195-196 (in part); Gray, 1825, Ann. Philos., n.s., vol. 10, p. 428 (in part); Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 19 (in part); A. Agassiz, 1872-1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, pp. 112, 531; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 159-160 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 398-400 (in part). Not de Blainville, 1834, d'Orbigny, 1854, Desor, 1858, Pomel, 1883, nor Lambert and Thiéry, 1914.

Echinoglycus van Phelsum, Leske, 1778, Add. ad Klein, pp. 197, 199, 201, 202, 204 (in synonymy, does not appear in van Phelsum as such) (in part).

Lobophora L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, pp. 64-65; L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, pp. 136-137 (in part); Desor, 1858, Synop. des échin. foss., p. 235. Not Curtis, 1825, nor Serville, 1839.

Tretodiscus Pomel, 1883, Class. method. et gén. échin. viv. et foss., p. 71. New name for *Echinodiscus* Leske and *Lobophora* L. Agassiz.

Tetrodiscus Pomel, Lambert and Thiéry, 1921-1925, Ess. nomencl. rais., pp. 323, 584-585. Corruption of *Tretodiscus* Pomel.

Type species: of *Echinodiscus*, *E. bisperforatus* Leske (by action of International Commission on Zoological Nomenclature; see Bull. Zool. Nomencl., vol. 4, p. 535, 1950); of *Echinoglycus*, *E. irregularis* Leske here designated (see discussion under *Encope*) = *E. bisperforatus* Leske; of *Lobophora*, *L. bifora*, L. Agassiz = *E. bisperforatus* Leske, subs. desig., Desor, 1858.

(Figs. 4, *a*; 5, *e* and *f*; 8, *b*; 32, *a*)

Medium-sized to large, flattened, thin; with 2 elongate, narrow, posterior ambulaeral lunules, either open or closed; oral surface flat, aboral surface slightly arched; margin thin; apical system central; petals well defined, nearly closed; anterior petal longest, posterior petals shortest; outer member of pore-pair greatly elongated, not subdivided; peristome central, small; ambulaeral food grooves bifurcating just outside basicoronal plates; periproct on oral surface, about one-fifth distance from ambitus; basicoronal plates of moderate size; interambulaeral plates very much larger than ambulaeral plates; usually first pair of post-basicoronal ambulaeral plates separates interambulaera from basicoronal plates; anterior paired interambulaeral with 3 or 4 post-basicoronal plates to column on oral surface; posterior paired interambulaera with 2 or 3 post-basicoronal plates to column on oral surface; posterior interambulaerum with 2 post-basicoronal plates to column on oral surface; periproct between first and second post-basicoronal plates; ambulaeral areas usually with 5 or 6 post-basicoronal plates to column on oral surface. Ambulaeral and interambulaeral areas about equal at ambitus, except for wider posterior interambulaerum.

Miocene to Recent, Indo-Pacific.

Specimens from the Miocene of India have the lunules more ovate than the Pliocene and Recent species, a characteristic that indicates the close relationship to *Amphiope*. However, the long anterior and short posterior petals, together with the elongate lunules easily separate *Echinodiscus* from *Amphiope*.

Genus *Amphiope* L. Agassiz

Amphiope L. Agassiz, 1840, Cat. syst. ectyp. échin., pp. 6, 17; 1841, Mon. d'Echin., See. Mon., Des Scutelles, p. 72; L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 136; Desor, 1858, Synop. des échin. foss., p. 235, Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 71; Lambert, 1907, Bull. Soc. Etud. Sci. Nat. Beziers, vol. 39, pp. 49-50; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 322; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 413-414.

Echinodiscus Leske, A. Agassiz, 1872-1873, Mem. Mus. Comp. Zoöl. Harvard Coll., vol. 3, pp. 112, 531 (in part); Dunean, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 159 (in part).

Type species: Amphiope bioculata L. Agassiz = *Scutella bioculata* Des Moulins, subs. desig., Lambert, 1907.

(Figs. 16, *d*; 32, *b*)

Medium-sized, flattened, with 2, usually transversely oval, posterior ambulaeral lunules; oral surface flat, aboral surface arched; apical system slightly anterior; petals well developed; moderately closed, more or less equal; outer member of pore-pairs greatly elongated, not subdivided; peristome slightly anterior; ambulaeral food grooves bifurcating just outside basicoronal plates; basicoronal plates well developed, interambulaeral plates much larger than ambulaeral plates; interambulaeral areas separated from basicoronal plates by first pair of post-basicoronal ambulaeral plates; interambulaeral areas normally with 2 or 3 post-basicoronal plates to column on oral surface; ambulaeral areas with 5 or 6 post-basicoronal plates on oral surface; innermost post-basicoronal interambulaeral plate usually somewhat elongated; posterior interambulaerum slightly wider, other interambulaera about same width as ambulaera at ambitus; periproct from one-fourth to one-fifth distance from margin, between first and second pair of post-basicoronal plates.

Oligocene to Miocene, Europe; Mioene, India.

The equally developed petals and lunules usually transversely oval are characteristic of the later species. In the Oligocene the lunules tend to be elongated radially.

Family Abertellidae n. fam.

Type genus: Abertella Durham.

Medium-sized to large, flattened; internal supports well developed; with broad ambulaeral and anal indentations of margin; petals well defined, nearly closed; outer member of pore-pair greatly elongated, few primary pore-pairs outside petals; all interambulaera discontinuous on oral surface; basicoronal interambulaeral plates considerably larger than ambulaeral plates; periproct submarginal; ambulaeral food grooves bifurcating just outside basicoronal row; 4 genital pores.

Miocene, Caribbean and Atlantic Coast of North America.

The well-defined anal indentation of the margin, the large basicoronal interambulaeral plates, and discontinuous interambulaera distinguish this monogeneric family from the Scutellidae (restricted).

Genus *Abertella* Durham

Abertella Durham, 1953, Jour. Paleont., vol. 27, pp. 350-351.

Type species: Scutella aberti Conrad, orig. desig.

(Fig. 32, *e*)

Large, thin, scutellid echinoids, rounded anteriorly, with moderately large posterior anal notch and broad marginal indentations in ambulaera I and V, shallower indentations at other ambulaera; petals elongate, moderately closed, length about two-thirds radius of test; pore-pairs conjugate, poriferous zones as wide as or wider than interporiferous zones; peristome of

moderate size, central; periproct submarginal, sometimes as much as one-eighth distance from margin (depending on depth of anal notch), situated along suture between second pair of post-basicoronal interambulacral plates; ambulacral food grooves of scutellid type but bifurcating closer to peristome than in *Parascutella*; basicoronal plates moderately small, ambulacral plates considerably larger and rounder than interambulacral plates; interambulacral columns widely separated from basicoronal interambulacral plates by first post-basicoronal ambulacral plates; on oral surface 3 or 4 post-basicoronal plates in each interambulacral column, 5 to 7 post-basicoronal plates in each ambulacral column; interambulacral areas only about half as wide as ambulacral areas at ambitus.

Miocene, Caribbean, and Atlantic Coast of North America.

Scutella floridana Cooke, *S. cazonesensis* Kew, and *S. habanensis* Sanchez Roig are other species to be referred to this genus. Kew was uncertain of the exact age of his species, but in view of its similarity to *S. floridana*, it would appear that it is probably of similar age. *S. habanensis* Sanchez Roig was referred to the "Oligo-Miocene" at the time of description and, in keeping with its older age, appears to be somewhat more primitive than the other species referred to the genus, for the posterior indentations of the test are less accentuated. In view of the fact that the other three species are apparently of Miocene age, it is probable that *S. habanensis* is also from beds of Miocene age rather than "Oligo-Miocene" age.

Abertella is easily separable from the European *Scutella* and *Parascutella* by its widely interrupted interambulacral areas on the oral surface. None of the Pacific Coast species referred to *Scutella* by Kew and others are closely related.

The relationship of *Echinarachnius sebastiana* Jackson (1922, pp. 48-50, pl. 7, figs. 5 and 6, text fig. 4), from the Oligocene of Porto Rico, to *Abertella* needs to be investigated, but no specimens were available for the present study.

Family Scutasteridae n. fam.

Type genus: Scutaster Pack.

Medium-sized to large, flattened, internal supports well developed; three more or less radially ovate anterior ambulacral lunules or indentations; petals well defined, moderately closed, anterior petal more widely open; a few primary pore-pairs outside petals; outer member of pore-pair greatly elongated; posterior interambulacrum discontinuous on oral surface, others apparently continuous; 4 genital pores; periproct submarginal; ambulacral food grooves bifurcating outside basicoronal row.

Lower Miocene, California.

The three anterior and no posterior ambulacral lunules make this a unique group. No other echinoid has evolved in this direction.

Genus *Scutaster* Pack

Scutaster Pack, 1909, Univ. Calif. Publ. Bull. Dept. Geol., vol. 5, p. 278; Stefanini, 1911, Boll. Soc. Geol. Ital., vol. 30, p. 757; Pack, 1913, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, pp. 300-301; Kew, 1920, Univ. Calif. Publ. Geol., vol. 12, p. 135; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 323; Grant and Hertlein, 1938, Univ. Calif. L. A. Publ. Math. Phys. Sci., vol. 2, pp. 94-95; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 451-452.

Type species: Scutaster andersoni Pack, monotypic.

(Figs. 31, *d*; 37, *a*)

Medium-sized to large, flattened, margins moderately thin; 3 anterior ambulacral lunules, closed to partially closed; test highest anterior to apical system; apical system slightly poste-

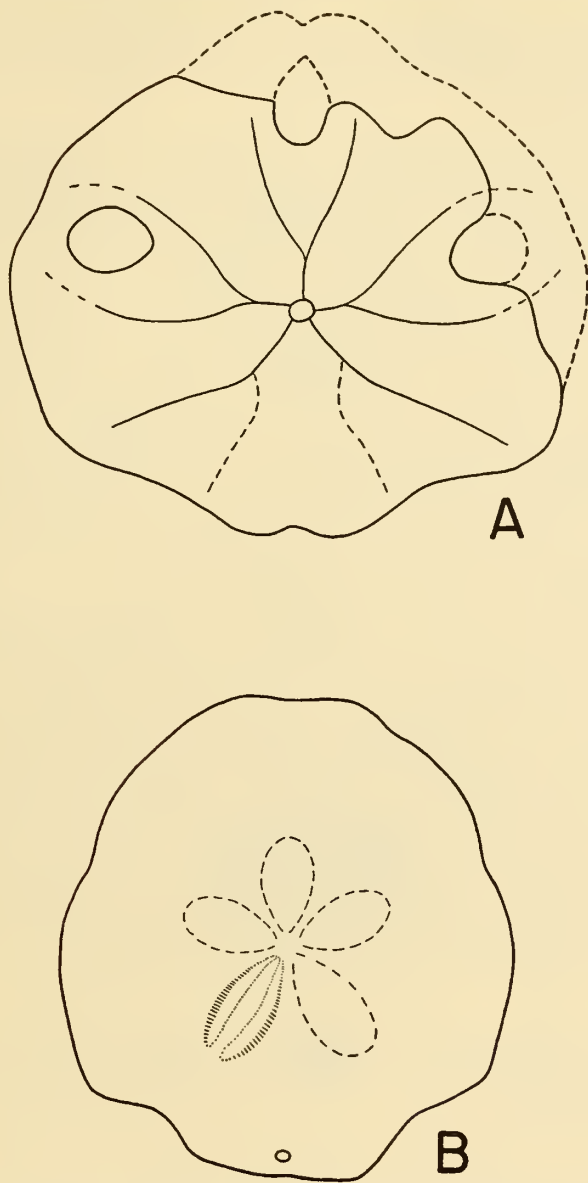


Fig. 37. *Scutaster* and *Scutulum*: a, *Scutaster vaquerosensis* Loel and Corey, $\times 1$, after paratype no. 31715, in part restored; lower Miocene, California. b, *Scutulum parisiense* Tournouër $\times 3$, diagrammatic, after two specimens in the collection of A. Chavan, Thoiry (Ain) France; lower Stampian, France.

rior; petals well developed, nearly closed posteriorly, moderately open anteriorly; outer member of pore-pair greatly elongated; peristome slightly posterior, small; ambulacral food grooves bifurcating outside basicoronal plates; basicoronal plates well developed, paired interambulacral plates much larger than ambulacral plates; 2 anterior basicoronal interambulacral plates much elongated, posterior plate very small; posterior interambulacrum separated from basicoronal plate by first post-basicoronal pair of ambulacral plates; paired interambulacra continuous; interambulacra about one-fourth width of ambulacra at ambitus; paired interambulacra with

3 or 4 post-basiceoronai plates to column on oral surface, posterior interambulacrum with 2 plates to column; periproct just inframarginal, between second post-basiceoronai pair of plates; 5 to 7 post-basiceoronai ambulacral plates on oral surface.

Lower Miocene, California.

This genus has been inadequately known ever since it was described by Pack. The type species is known only from a single specimen (holotype, U.C.M.P. no. 11029) from the type locality in central California. The specimen figured by Pack (1913) as *S. andersoni* does not appear to be conspecific with the holotype. An examination of the matrix adhering to the oral surface of the type indicates that it is from the San Ramon formation of upper Oligocene age. The type of *S. andersoni* is incomplete, two petals, the apical system, and the posterior margin being missing, and the oral surface is covered with matrix. Comparison with Pack's 1913 figure of the specimen from the Mount Pinos quadrangle indicates that the latter has much more marked indentations in the margin next to the ambulacral lunules and differently proportioned (height: width ratio) plates in the anterior interambulacra. The Mount Pinos quadrangle specimen probably represents another species. It appears noteworthy that all other species referred to this genus have been recorded from south of the transverse ranges.

Not much additional data can be obtained from the holotype of *S. andersoni*. The margins were very thin. The ambulacral areas widen greatly beyond the petals, so that the interambulacral areas are comparatively narrow. Apparently there were eleven plates in the posterior column of interambulacrum 4 (apical system missing, but column appears complete) on the aboral surface. Probably there were ten plates in the posterior column of interambulacrum 3 (incomplete).

Several specimens of *S. vaquerosensis* Loel and Corey are available. There are four genital pores. The madreporite is rather large, extending well out into the interambulacral areas. The interporiferous area of the petals is slightly raised. The ambulacral food grooves are bifurcating, and there are broad grooves on the oral surface from the lunules toward the small peristome. The oral surface is slightly arched, and the periproct is immediately submarginal.

Family *incertae cedis*

Because of lack of material, poor material, or inadequate descriptions, the following genera have not been placed in families, although they all seem to be referable to the Scutellina.

Genus *Scutulum* Tournouër

Scutulum Tournouër, 1869, Bull. Soc. Géol. France, ser. 2, vol. 26, p. 981; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 317; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 387.

Scutellum Fritel, 1910, Guide géol. pal. Rég. Paris, p. 209 (error for *Scutulum*). Not Pusch, 1833.

Type species: *Scutulum parisiense* Tournouër, monotypic.

(Fig. 37, b)

This genus is based on a single species from the Stampian of the Paris Basin that has never been adequately figured. Two specimens lent for examination by Dr. André Chavan are so poorly preserved that the structure of the test cannot be determined. The genus apparently may be characterized as follows (on p. 182).

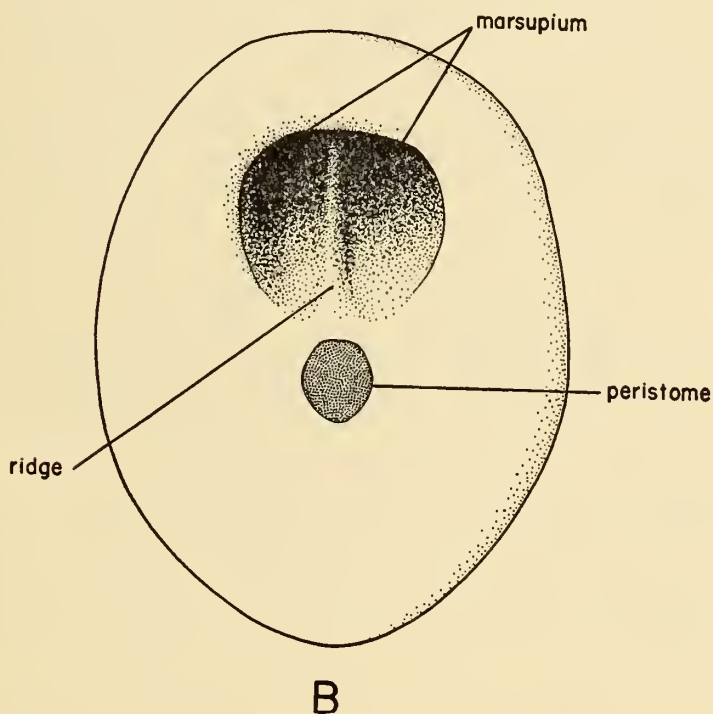
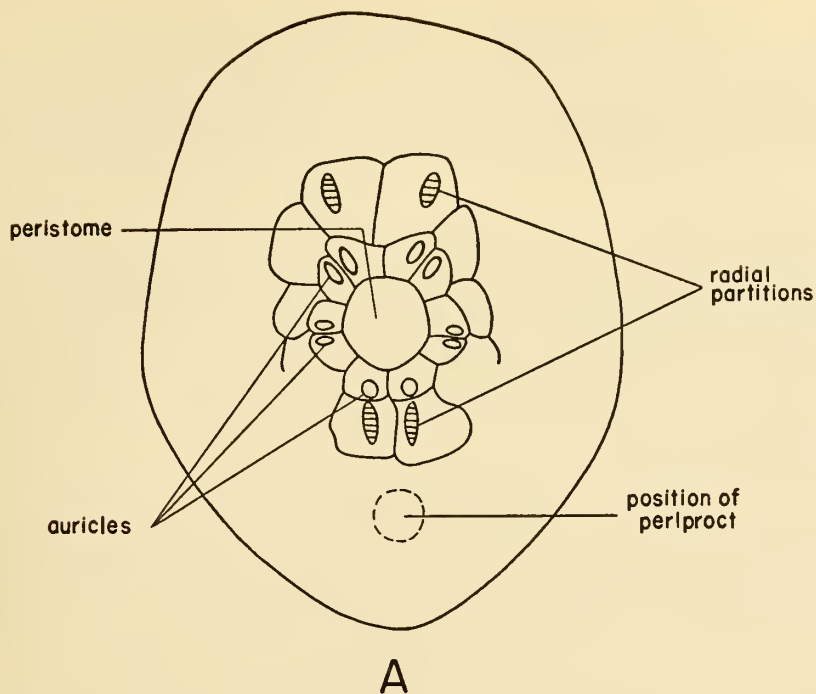


Fig. 38. *Fossulaster halli* Lambert and Thiéry, lower Miocene (?), Australia: *a*, male, $\times 9$, after British Museum (Natural History) paratype no. E 9865; oral surface from interior, showing auricles, two pairs of inner radial partitions, outline of some plates, and superimposed position of aboral periproct; basicoronal interambulaeal plates not visible from interior. *b*, female, $\times 8$, after British Museum (Natural History) lectotype no. E 9864; oral surface from exterior, showing marsupium and longitudinal ridge.

Small, thin, flattened scutellid echinoids; ambitus indented in ambulacral areas, petals short, broad, slightly less than half length of radius of test, moderately closed; outer pore of pore-pairs greatly elongated; apical system slightly raised; 4 genital pores; periproct supramarginal; peristome central, moderately small; ambulacral food grooves bifurcating about one-third radius of test from peristome.

Oligocene, France.

Mortensen doubts whether this genus is distinct from *Samlandaster* Lambert and Thiéry, which is based on the upper Eocene *Scutella germanica* Beyrich, a species with a supramarginal periproct but with a rounded outline. However, Noetling's (1885-1888) figures of Beyrich's species show the inner and outer pores of the petals to be approximately equal in size and not greatly elongated. This latter difference, in addition to the differences in shape, indicates that the two genera are not closely related.

Genus *Proescutella* Pomel

Proescutella Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 70.

Proescutella Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 130; Cotteau, 1891, Paléont. Franc., Terr. Tert., vol. 2, pp. 254-255; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 315; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 395-396.

Type species: *Scutella cailliaudi* Cotteau, orig. desig.

(Fig. 28, e)

Medium-sized scutellid echinoids; oral side flattened, aboral side raised, margins moderately thin; petals open, length about four-fifths radius of test; pore-pairs apparently not conjugate (?); outer member of pore-pair slightly elongate; 4 genital pores; peristome of moderate size, central; periproct on oral surface, about one-fourth distance from margin; ambulacral food grooves simple, well defined, extending to margin; interambulacral areas narrow, less than half the width of ambulacral areas at ambitus; numerous plates in both ambulacral and interambulacral areas on oral surface; details of basicoronal row uncertain; periproct apparently between sixth pair of post-basicoronal plates (after Cotteau, 1891, pl. 266, figs. 3, 11, 12).

Eocene, France.

The type species is from the middle Eocene of the Lower Loire basin, France. Cotteau (1891, pp. 259-261) described *P. degrangei* from the middle Eocene of Gironde as a member of this genus; it was referred to *Echinodiscus* [*Laganum auctores*] by Lambert and Thiéry (1914, p. 311), but this was wholly unwarranted. Although this species differs from *P. cailliaudi* in having an indented margin, somewhat wider interambulacral areas on the oral surface, and definitely conjugate pore-pairs, it probably belongs in *Proescutella*.

Proescutella cossmanni Lambert (1901) from the Parisian Eocene was subsequently referred to *Astrodapsis* Conrad by Lambert and Thiéry (1914, p. 314), but it has no relationship to that genus. It appears to represent a new genus which may be differentiated from *Proescutella* by its shorter petals, marginal periproct, and fewer plates on the oral surface; but Lambert's figures are inadequate for a proper diagnosis.

Genus *Samlandaster* Lambert and Thiéry

Samlandaster Lambert and Thiéry, 1914, Ess. nomencl. rais., pp. 293-294; Lambert, 1915, Actes Soc. Linn. Bordeaux, vol. 79, p. 29; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 387-388.

Type species: *Scutella germanica* Beyrich, monotypic.

Small, thin, very flattened scutellid echinoids; outline rounded, margins thin; petals short,

narrow, length about one-third radius of test, moderately closed; both pores of pore-pairs about equal in size, only slightly elongated; genital pores 4; periproct supramarginal, small; peristome central, small; ambulacral food grooves bifurcating a short distance from peristome; internal supports highly developed.

Upper Eocene, Samland, northern Germany.

The rounded outline, subequal pores in petals, and food grooves bifurcating close to the peristome appear to be characteristics which would suffice to separate this genus from *Scutulum* Tournouër, despite the fact that *S. parisiense* is very poorly known. *Scutella germanica* Beyrich has been well figured by Noetling (1885-1888).

Suborder ROTULINA Gray, emended

Rotulinae Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 65 (in part); Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 321 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 452.

Test flattened, posteriorly dentate or digitate; moderately well developed internal supports; primary pore-pairs restricted to aboral surface, usually conjugate; petals (fig. 1, *a* and *b*) well defined, open; ambulacral plates all primaries, much smaller in petals than on oral surface; posterior interambulacrum continuous; interambulacra about as wide as ambulacra at ambitus; interambulacra (fig. 12, *c*) terminate adapically in series of single plates; apical system compact, stellate, apices (fig. 1, *b*) of rays corresponding to ambulacral areas; 4 genital pores; apical system and peristome opposite, central; buccal membrane (fig. 8, *h*) plated; periproct on oral surface; basicoronal plates 20, with 5 interambulacral plates more or less reduced; basicoronal interambulacral plates as large as or larger than ambulacral plates; auricles fused; primary spines (fig. 5, *k* and *l*) short, club-shaped; aboral miliary spines (fig. 6, *i*) smooth, terminating in a crown; 3 spicules (fig. 8, *c*) in sucking disc of tube feet.

Miocene to Recent, tropical west coast of Africa.

The characters of the basicoronal row, apical system, head of the interambulacra, miliary spines, and tube feet preclude associating this small group with any of the other suborders recognized.

The earliest recorded species occurs in the Miocene of Angola (Darteville, 1940, pl. 2, figs. 3 and 4, legend).

Family Rotulidae Gray, emended

Rotulinae Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 65 (in part); Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 321 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 452.

Diagnosis same as for the suborder.

Genus *Rotula* Schumacher

Echinodiscus, Leske, 1778, Add. ad Klein, pp. 195-196 (in part); Gray, 1825, Ann. Philos., n.s., vol. 10, p. 428 (in part); d'Orbigny, 1854, Rev. et Mag. Zool., ser. 2, vol. 6, pp. 19, 26 (in part). Not Desor, 1858, nor Lambert and Thiéry, 1914.

Rotula Schumacher, 1817, Ess. hab. vers test., pp. 33, 84 (in part); L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, p. 23 (in part); L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 138 (in part); Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 16 (in part); Desor, 1858, Synop. des échin. foss., p. 238; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 163-164 (in part); Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 321; Darteville, 1940, Inst. Roy. Col. Belge Bull., vol. 11, pp. 184-189; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 454 (in part).

Echinotrochus Pomel, 1883, Class. method. et gén. échin. viv. et foss., p. 72.

Type species: of *Rotula*, *Echinodiscus octiesdigitatus* Leske = *Rotula multiloba* Schumacher = *Rotula augusti* Klein (pre-Linnaean) = *Echinus orbiculus* Linnaeus, var., subs. desig., Desor,

1858 (*Echinodiscus octiesdigitatus* Leske is considered to be a variant of *E. deciesdigitatus* Leske by Mortensen and others); of *Echinotrochus* Pomel, *E. augusti* Klein = *Echinodiscus octiesdigitatus* Leske, monotypic.

(Figs. 1, *b*; 2, *b*; 5, *l*; 19, *d* and *e*; 28, *f*)

Medium-sized, flattened, posteriorly digitate, with paired elongate anterior interambulacral lunules; oral surface flat, aboral surface arched, greatest height anterior to apical system; apical system central, small; petals well formed, open, anterior petal most widely open; pore-pairs conjugate, outer pore elongated and subdivided; peristome central, small; ambulacral food grooves bifurcating on basicoronal plates; three posterior interambulacral indentations deepest, actually unclosed lunules corresponding to anterior lunules; remaining indentations variably developed, occur along radial sutures; periproct oral, about one-third distance from inner end of middle posterior indentation, between first pair of post-basicoronal plates; basicoronal plates of moderate size, 5 interambulacral plates about equal to ambulacral plates, 5 interambulacral plates reduced in size; paired interambulacra normally separated from basicoronal row by first pair of post-basicoronal ambulacral plates; posterior interambulacrum in contact with basicoronal plates; interambulacra with 5 or 6 post-basicoronal plates per column on oral surface; ambulacra with 5 to 7 plates per column on oral surface; ambulacra about as wide as interambulacra at ambitus.

Miocene to Recent, tropical west coast of Africa.

The living rotulids have been considered to represent two separate genera by Desor (1858), Pomel (1883), Lambert (1907), Lambert and Thiéry (1921), Cottreau (1923), Darteville (1940), and others; but A. Agassiz, Duncan, Koehler, H. L. Clark, and Mortensen have referred them all to a single genus. Nevertheless, from Mortensen's text it is apparent that he recognized the significant differences between the two species but referred them both to the same genus, *Rotula*, as a matter of convenience. The presence of closed lunules in the anterior interambulacra of *R. deciesdigitata* is a major character which in all other clypeasteroids has been considered of generic significance. In addition, the outer pore of the petals is broken up into several small pores in this species but is undivided in *orbiculus*. Correspondingly, the pores are only faintly conjugate in *deciesdigitata* but are distinctly conjugate in *orbiculus*. It is well to note also that in *deciesdigitata* there are actually five interambulacral lunules present, those of the three posterior interambulacra not having closed. However, in some individuals the three posterior lunules are almost closed. In *orbiculus* the posterior digitations of the test are formed by simple indentations along the sutures between the various columns of plates. In *deciesdigitata* the three posterior indentations in the mid-line of the interambulacra are at least half again as deep as the other indentations; whereas in *orbiculus* the indentations are all of approximately the same depth. It would appear that *deciesdigitata* may have had five well-developed lunules before the remaining posterior indentations of the test appeared.

Examination of the plates around the peristome of *R. deciesdigitata* (fig. 19, *d* and *e*) shows a very unusual situation. The basicoronal row contains twenty plates, instead of the fifteen normally present in the other clypeasteroids. Of these twenty plates, 1a, 2a, and 4b are reduced in size, and on some specimens, when seen from the exterior, are highly reduced (fig. 19, *d*). It is to be noted that the sutures are not always normal to the surface, and that consequently the outlines of the same plates may vary when seen from the inside of the test instead of the outside (fig. 19, *e*). Without a complete series of specimens from young to adult sizes, it is im-

possible to properly evaluate the significance of these extra five plates. But from the condition existing in *Heliophora orbiculus*, in which the extra plates are well developed at a diameter of 10 mm. and later become reduced, it appears possible that there may be two primary interambulacral plates in this group, but it is even more probable that the second interambulacral plate is pushed into the basicoronal row at a very early stage in the ontogeny. Under either hypothesis this appears to be of considerable taxonomic significance.

Dartevelle (1940, pl. 3) has strikingly illustrated the variable development of the posterior indentations. In all cases the posterior interambulacral "lunules" are fully developed, but in some the intermediate indentations are merely incipient.

The typical species lives along the west coast of Africa from Gambia to Angola. Except for Dartevelle's (1940) record from the Miocene of Angola, the genus does not appear to have been recorded as a fossil. Dartevelle referred the fossil specimens to the living species; but from his figures it appears that the posterior interambulacral lunules (in the sense discussed above) are not as deep as in the living form.

Genus *Heliophora* L. Agassiz

Echinodiscus Leske, 1778, Add. ad Klein, pp. 195-196 (in part); Gray, 1825, Ann. Philos., n.s., vol. 10, p. 428 (in part); d'Orbigny, 1854, Rev. et Mag. Zool., ser. 2, vol. 6, pp. 19, 26 (in part); Desor, 1858, Synop. des échin. foss., p. 238. Not A. Agassiz, 1872-1873, nor Lambert and Thiéry, 1914.

Heliophora L. Agassiz, 1840, Cat. syst. ectyp. échin., p. 17; Lambert, 1906, Mém. Soc. Géol. France, Paléont., vol. 14, fasc. 2-3, p. 126; Cottreau, 1923, Ann. Paléont., vol. 12, pp. 140-145. Not *Heliophorus* Geyer, 1832.

Rotula Schumacher, 1817, Ess. hab. vers test., pp. 33, 84 (in part); L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, p. 23 (in part); L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 138 (in part); Gray, 1855, Cat. Rec. Echin. Brit. Mus., pt. 1, p. 16 (in part); Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, pp. 163-164 (in part); Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, p. 454 (in part).

Hemiheliopsis Lambert, 1906, Mém. Soc. Géol. France, Paléont., vol. 14, fasc. 2-3, p. 128; Cottreau, 1923, Ann. Paléont., vol. 12, pp. 144-145.

Radiorotula Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 321.

Type species: of *Heliophora*, *Rotula rumphii* Klein = *Echinus orbiculus* Linnaeus var. *a*, subs. desig., Lambert, 1906; of *Hemiheliopsis*, *H. fonti* Lambert, monotypic; of *Radiorotula*, *Echinus orbiculus* Linnaeus = *Rotula rumphii* Klein, orig. desig.

(Figs. 1, *a*; 5, *k*; 6, *i*; 8, *h*; 10, *d*; 12, *c*; 15, *d*; 19, *a-c*, *g*; 26, *m*)

Medium-sized, flattened, posteriorly digitate, no lunules; oral surface flat, aboral surface arched, greatest height at apical system; apical system central, small; petals well formed, open, anterior petal most widely open; pore-pairs conjugate, outer pore slightly elongated, not subdivided; peristome central, small; ambulacral food grooves bifurcating on basicoronal plates; posterior indentations equally deep except outermost; periproct on oral surface about one-third distance from indentation, between first pair of post-basicoronal plates; basicoronal plates of moderate size, principal series of interambulacral plates larger than ambulacral plates, secondary series of interambulacral plates not as reduced as in *Rotula*; paired interambulacra usually separated from basicoronal plates by first post-basicoronal ambulacral plates, but considerable individual variation; posterior interambulacrum in contact with basicoronal plate; 4 or 5 post-basicoronal plates per column on oral surface in paired interambulacra, 6 plates per column in posterior interambulacrum; usually 5 or 6 post-basicoronal ambulacral plates per column on oral surface; interambulacra about as wide as ambulacra at ambitus.

Miocene to Recent, tropical west coast of Africa.

The lack of interambulacral lunules (see discussion under the genus *Rotula*) clearly separates this genus from *Rotula*. As in *Rotula deciesdigitata* there are twenty plates around the peristome in *H. orbiculus* (fig. 15, *d*). This condition is visible in the smallest available specimens (10 mm. in diameter). In the adult, the extra basicoronal plates appear to be derived from the posterior column of each paired interambulacrum and from the right-hand column (when viewed from aboral side) in interambulacrum 5. However, examination of the young individual 10 mm. in diameter (fig. 19, *a*) indicates the possibility that the inserted plates are derived from the other column and that the auricles have moved onto the inserted plates. Younger individuals than those now available are needed to determine precisely the origin of these extra interambulacral plates in the basicoronal row. In small individuals, the interambulacral columns are all in contact with the basicoronal row, but in the adult only interambulacrum 5 is always in contact with the basicoronal plate.

The type species occurs along the African coast from Senegal to Angola and has been recorded from Ascension Island, Cape Verde, and Saint Thomas. The species *fonti* has been recorded from the Pliocene of Río de Oro (as *Hemiheliopsis*). Darteville (1940, pp. 179–180, pl. 11, figs. 9 and 10) has recorded the type species from beds near Loanda which have been assigned a Miocene age. However, he suggests that, because of the resemblance of the fossils to the living species, the particular strata in which the echinoids occur are perhaps younger.

Darteville (*op. cit.*, p. 191) has noted that the rotulids have a mode of life similar to that of *Dendraster excentricus*, and that they live partly buried in the substratum, with the digitate posterior part of the test extending up into the water. He suggested that the posteriorly divided test gives less resistance to water currents, so that it is easier for the individual to maintain a semiupright position.

Genus *Rotuloidea* Etheridge

Rotuloidea Etheridge, 1872, Quart. Jour. Geol. Soc. London, vol. 28, p. 98; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 148; Lambert and Thiéry, 1921, Ess. nomencl. rais., p. 321; Cottreau, 1923, Ann. Paléont., vol. 12, p. 4; Mortensen, 1948, Mon. Echin, vol. 4, pt. 2, p. 453.

Type species: Rotuloidea fimbriata Etheridge, monotypic.

(Fig. 19, *f*)

Medium-sized, oral surface flat, aboral surface fairly strongly arched, margin thick; posterior margin "scalloped," anterior margin entire; greatest height at apical system; apical system central, small; petals well formed, open, anterior petal most widely open; pore pairs only partially conjugate; outer member of pore-pair moderately elongate, not subdivided; peristome slightly posterior; ambulacral food grooves bifurcating on basicoronal plates; periproct approximately midway on oral surface, at junction between first and second pair of post-basicoronal plates; basicoronal plates of moderate size, major interambulacral plates larger than ambulacral plates, secondary plates variably reduced in size; interambulacra all continuous on oral surface; interambulacra with 5 to 7 post-basicoronal plates to column on oral surface; ambulacra with 6 or 7 plates to column on oral surface; interambulacra and ambulacra about equal in width at ambitus.

Lower Pliocene, Morocco.

This genus has been excellently treated by Cottreau, who had an abundance of material. It is closely related to *Heliophora* Agassiz; but if Darteville's (1940,

pp. 179–180) records of the latter from Angola are from beds which are correctly assigned a Miocene age, then *Rotuloidea* cannot be ancestral to *Heliophora*. The thicker margin, the slightly lobed instead of digitate posterior margin, the more open and longer petals, and the continuous interambulacra differentiate *Rotuloidea* from *Heliophora*. A young *Heliophora* is very similar to an adult *Rotuloidea* (fig. 19, *f* and *g*). The genus has been recorded only from the lower Pliocene of Morocco.

Suborder *incertae cedis*

Genus *Runa* L. Agassiz

Runa L. Agassiz, 1841, Mon. d'Echin., Sec. Mon., Des Scutelles, p. 32; L. Agassiz and Desor, 1847, Ann. Sci. Nat., ser. 3, vol. 7, p. 139; Desor, 1858, Synop. des échin. foss., p. 221; Pomel, 1883, Class. méthod. et gén. échin. viv. et foss., p. 73; Duncan, 1889, Jour. Linn. Soc. London, Zool., vol. 23, p. 147; Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 294; Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 167–168 (in part).

Type species: *Runa comptoni* L. Agassiz, subs. desig., Lambert and Thiéry, 1914.

These internal molds, as Lambert and Thiéry, and Mortensen have noted, are probably the internal mold of fibularine echinoids. Undoubtedly the adults are known under other names. Mortensen (1948, p. 233, fig. 144) has again presented Noetling's illustration of the internal mold of *Lenita patellaris*. The figure closely resembles that of *Runa desori* Michelotti. It should be noted that, if the identity of *Runa comptoni* with some other named and identifiable species is ever established, *Runa* is an available generic name. In the meantime it is best considered a *nomen vanum*.

The type species is from the Miocene of Italy.

Genus *Tournoueraster* Lambert

Tournoueraster Lambert, Lambert and Thiéry, 1914, Ess. nomencl. rais., p. 294; Lambert, 1915, Actes Soc. Linn. Bordeaux, vol. 69, p. 18.

Runa L. Agassiz, Mortensen, 1948, Mon. Echin., vol. 4, pt. 2, pp. 167–168 (in part).

Type species: *Scutella decemfissus* Des Moulins, orig. desig.

This genus has the same status as *Runa* but obviously represents a different genus and probably a different family from *Runa*. The type is from the Stampian of France.

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PLATES

PLATE 3

Plate arrangement and growth lines of various echinoids

1, 2. *Scutellaster interlineatus* (Stimpson), $\times 0.6$. Oral and aboral views of weathered specimen showing plate arrangement. Cal. Acad. Sci. hypotype no. 9964. Pliocene, California.

3. *Mellitella* sp., $\times 1.3$. Aboral view of weathered specimen showing growth lines. Hypotype no. 33431. Miocene, Venezuela.

4. *Pericosmus* sp., $\times 1.1$. Aboral view of weathered specimen showing growth lines. Hypotype no. 33433. Miocene, Venezuela.

5, 7. *Scutellaster interlineatus* (Stimpson). Aboral views of weathered specimens showing growth lines. Fig. 5, hypotype no. 33866, $\times 0.80$. Fig. 7, hypotype no. 33867, $\times 0.86$. Pliocene, California.

6. *Arbaeia* sp., $\times 1.3$. Aboral view of Recent specimen artificially abraded showing growth lines. Photographed by transmitted light. Hypotype no. 33434. Recent, locality unknown.

8. *Scutellaster interlineatus* (Stimpson), $\times 1.3$. Aboral view of partially polished specimen showing growth lines. Hypotype no. 33923. Photographed under glycerine. Pliocene, California.

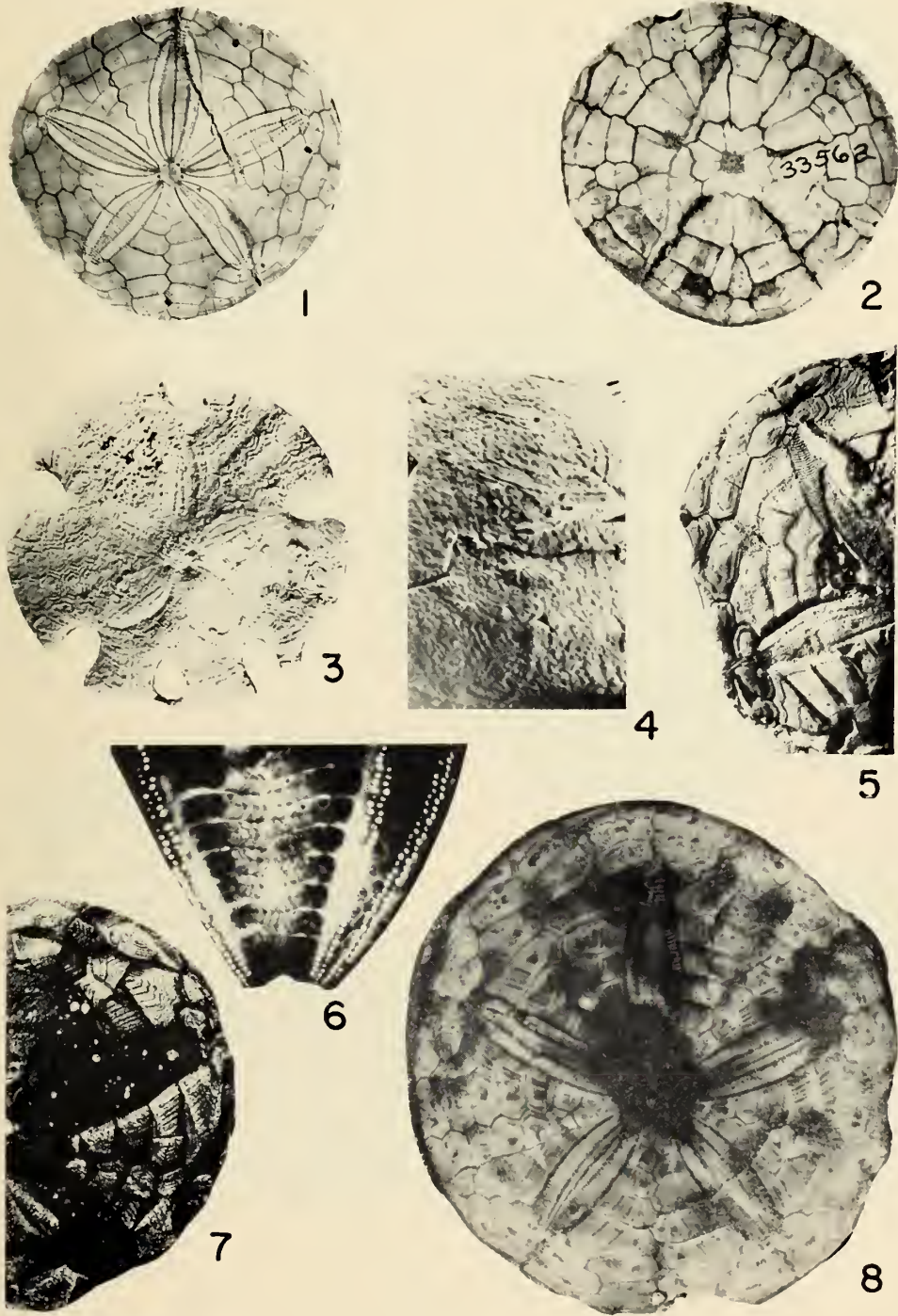


PLATE 4

Growth lines of various echinoids

1. *Mellita quinqueisperforata* (Leske), $\times 1$. Aboral view showing growth lines. Treated with "Clorox," stained and photographed with transmitted light. Hypotype no. 33436. Recent, Gulf of Mexico.

2, 3, and 6. *Strongylocentrotus franciscanus* (Agassiz). Growth lines. Fig. 2, hypotype no. 33438a, $\times 0.8$. Recent, California. Plates near the ambitus artificially abraded. Photographed first by transmitted, then by reflected, light. Figs. 3 and 6, plates near the peristome artificially abraded and etched with dilute hydrochloric acid. Photographed by reflected light. Fig. 3, hypotype no. 33438b, $\times 1.2$. Fig. 6, hypotype no. 33438c, $\times 1.4$.

4. *Echinarachnius parma* (Lamarek), $\times 1.5$. Aboral view showing growth lines. Treated with "Clorox." Photographed by transmitted light while damp. Hypotype no. 33440. Recent, Woods Hole, Mass.

5. *Scutellaster interlineatus* (Stimpson), $\times 1.5$. Oral view of weathered specimen, with growth lines showing asymmetrical growth causing changes in the relationship of plates during ontogeny. Hypotype no. 33870. Pliocene, California.



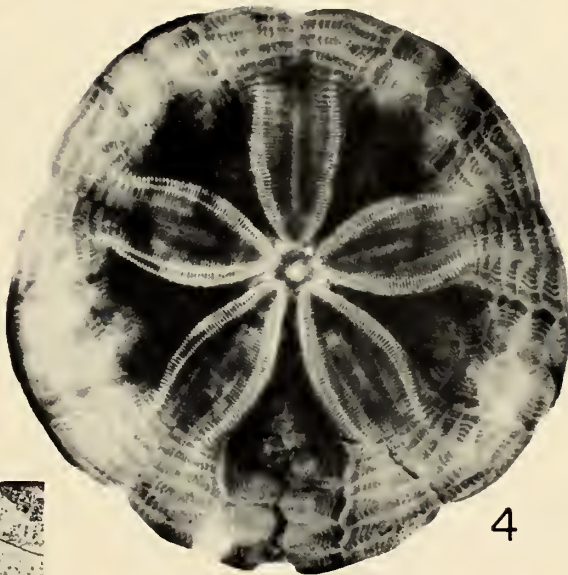
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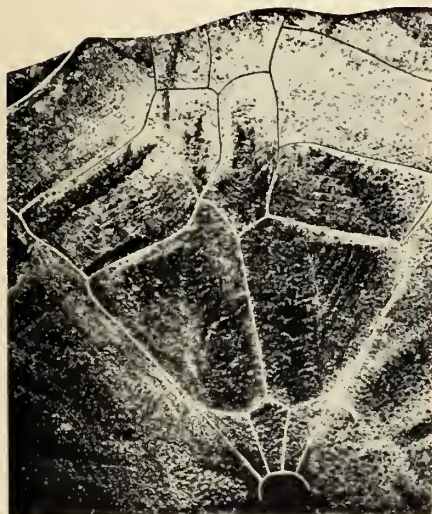
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